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Issued under the authority of
The Honourable Arthur Laing, P.C., M.P., B.S.A.
Minister of Northern Affairs and National Resources

DEPARTMENT OF NORTHERN AFFAIRS AND NATIONAL RESOURCES
OTTAWA 1963

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OTTAWA, 1963

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STELLARIA LONGIPES GOLDIE AND ITS ALLIES IN NORTH AMERICA

By A. E. Porsild

For the treatment of the genus *Stellaria* in manuals, now in preparation, on the floras of the Mackenzie District, N.W.T., and the southern Canadian Rocky Mountains, a review is necessary of the present taxonomic status and the geographic ranges of members of that notoriously perplexing, essentially North American *"Artenkreis"* or "complex" centring around *Stellaria longipes* Goldie, the first North American taxon within this group to be formally recognized, having been discovered "in woods near Lake Ontario" in 1819 by John Goldie and published three years later by him.

In 1823 the high-arctic *S. Edwardsii* was described by Robert Brown from specimens brought back by Parry's 1st Voyage from Melville Island in the Canadian Arctic Archipelago. Later in the same year appeared *S. nitida,* described by W. J. Hooker from East Greenland. In 1824 Seringe, in DeCandolle's Prodromus, added *S. Laxmanni* Fisch., *S. falcata* Ser., and *S. dahurica* Willd. from Siberia, and in 1830 W. J. Hooker, in Fl. Bor.-Am., treated the *Stellariae* collected in North America by members of the first two Franklin Expeditions, adding *S. laeta* Richards. and *S. stricta* Richards. to the fast-growing list. The same year, Bunge in Ledeb. Fl. Altaica, Vol. 2, added *S. pedunculata,* and in greater detail in 1842, Fenzl, in Ledebour's Fl. Rossica, discussed and re-defined most of these taxa. In North America, Sereno Watson (1878) reduced some of those proposed for North America to synonymy, and others to varieties of *S. longipes*, and finally in 1895, Index Kewensis, Fasc. iv, listed *S. Edwardsii, S. laeta, S. nitida, S. peduncularis,* and *S. stricta* as synonyms of *S. longipes* Goldie.

Because *S. longipes* s. str. is the only member of the group occurring within the ranges of the well-known North American manuals dealing with temperate floras, their authors have not needed to concern themselves with the interpretation of other members of the group, and only Rydberg (1917, 1922, and 1932) in his manuals on the floras of Rocky Mountains and Prairies and Plains has taken up *S. laeta, S. Edwardsii, S. stricta,* and *S. subvestita* Greene. A still more recent addition to the group is *S. arenicola* Raup, thus far known only from northwestern Saskatchewan.

In the absence of a monographic treatment, botanists dealing with the floras of arctic North America, including Greenland, until recently have contented themselves with considering *S. longipes* a plastic species represented in the Arctic by several poorly defined and unstable races or ecotypes.

W. J. Hooker fully realized the difficulties presented by this group when, in Fl. Bor.-Am., he wrote about *Stellaria longipes*: "The present *Stellaria* is one (along with 4, 5, and 6) [*S. stricta, S. laeta*, and *S. Edwardsii*] of a series of the genus, respecting which I scarcely know whether they should constitute species or rather be described as varieties. Characters, indeed, may easily be detected for defining the extreme appearances of them: but there are, among the numerous specimens which Dr. Richardson's and Mr. Drummond's rich collections can boast, intermediate states which I cannot satisfactorily refer to any. All are distinguished by their rigid erect habit; (except the var. α of the present species) by leaves, broad at the base, gradually tapering upwards, by their remarkable glossiness, unless when any portion, or the whole of them, be glaucous; by their obscurely-nerved calyx; and by the large, deep, rich, brown, or black, very glossy, capsule, which, being longer than the calyx, forms a striking contrast with the pale hue of the rest of the plant. Our present species is distinguished by a larger size than the rest, by its more distant, longer leaves, and especially by the great length of the pedicels of its flower and fruit. Nevertheless, the plants of a humbler growth border upon Dr. Richardson's and our *S. laeta,* which, however, differs in its yet smaller size, shorter foliage, and more acute sepals."

Basing his remarks on field observations of *S. longipes* in the Eastern Canadian Arctic, Polunin (1940) noted: "Except concerning the colour of the capsule and the glaucosity of the leaves—which characters may change completely without any obvious cause—I agree with Scholander (1934, p. 49) [who wrote about *S. longipes,* in Spitsbergen] that 'the habitat seems to be largely responsible for most of the variations'."

In his important paper *"Stellaria longipes* Goldie and its allies," Hultén (1943), mainly on the basis of the kinds of pubescence found on the sepals, and on the presence or absence of scarious bracts in the inflorescences, was able to recognize six species within the group, for which he claimed more or less distinct geographical ranges. The revision was made during World War II when Hultén, unfortunately, was unable to secure adequate North American and Asiatic material for comparison or to examine type material in the herbaria of London, Berlin, or Leningrad. In dealing with the North American races of *S. longipes,* it is especially unfortunate that he apparently lacked material of *S. stricta, S. subvestita,* and *S. arenicola.*

Böcher (1951), on the basis of Hultén's treatment, revised the large material of *S. longipes* s. lat. in the herbaria of Copenhagen and Oslo. dealing particularly with distribution and ecology of the taxa represented in the flora of Greenland, to which he added recent chromosome counts for *S. longipes* s. str. (2n=54), *S. crassipes,* and *S. monantha* (2n=104) and *S. ciliatosepala* [*S. Edwardsii*] (2n=91).

In order to test Hultén's treatment on the basis of a larger and more representative North American material than had been available to him, the writer, in 1953, using Hultén's key, sorted the 440-odd specimens of North American *S. longipes* s. lat. then in the herbarium of the National Museum of Canada, plotting the ranges of each taxon. In the following years some additional 300 specimens have been examined, and the information has been entered on maps.

Since Hultén's key is clear-cut and unequivocal, this sorting presented no difficulties as regards the bulk of the material. The three western species of which Hultén had reported no material, all according to his key fell into the pile of *S. longipes* s. str. A residual lot of some 50-odd sheets could not be keyed out because of combinations of characters not provided for in the key. This difficulty had already been experienced by Raup (1947) who, when writing about *S. Edwardsii* (*sensu* Raup) in the Mackenzie Mountains (Brintnell Lake), N.W.T., wrote: "In our plants, however, the pubescence on the sepals is quite variable as to presence and quantity. Many plants in the same colony will vary from sepals pubescent to quite glabrous. My personal experience with plants of the *S. longipes* group strongly suggests that entities found in it are hardly worthy of specific rank. Their geographic segregation, however, suggests that they should be considered as something more than forms."

An examination of duplicate sheets in the National Herbarium of Canada, of Raup's collection cited (l.c.) from Brintnell Lake, fully confirms the first part of the above statement. In none of the plants are scarious bracts present. Raup's No. 9191 agrees perfectly with *S. monantha* var. *altocaulis* Hult. from Yukon and central Alaska; No. 9413, from a high-alpine rock slide, is more condensed, and in all but one plant the sepals are glabrous. In No. 9349, also from a rock slide, the material is very homogenous, and clearly all came from one clone or mat; however, in nine of the twelve flowers present on the duplicate sheet, the sepals are perfectly glabrous while in the remaining three, they are densely pubescent on the back. Number 9834, from shale cliffs in a gorge, from elevation of only 3,500 feet, also is quite homogenous; all specimens have ciliate sepals and pale, stramineous capsules in varying degrees of maturity; a few dehizing ones are twice as long as the 4-mm-long calyx. Finally, in No. 9206, from an alpine meadow, the sepals are very short ciliate, in the manner of *S. Edwardsii*, but, as in the other numbers, scarious bracts are lacking in the inflorescence.

Under *S. ciliatosepala*, Böcher (l.c.) discusses specimens seen by him from northern East and West Greenland and from the eastern Canadian Arctic Archipelago, having various combinations of characters involving scarious bracts in the inflorescence and pubescent sepals. He points out that plants having these combinations appear to be restricted to areas believed to have been unglaciated in Pleistocene time and, therefore, may represent an ancient element in the flora with a relict type of distribution. Among the specimens cited by Böcher, I have seen only one (N.W. Greenland, lat. 77° 47′ N., Igdloluarsuit, Aug. 9, 1921, leg. Nygaard), of which a duplicate is before me. It is of tall and rank growth, as is commonly the case with specimens from heavily manured habitats. The plants are totally glabrous, except for the ciliate-margined and pubescent sepals; the long peduncles of the mostly solitary flowers are supported by normal, non-scarious margined leaves. Specimens perfectly matching the Igdloluarsuit plants were collected below a bird rookery on Little Diomede Island in Bering Strait (Porsild and Porsild, No. 1685, CAN).

A number of specimens, intermediate between *S. Edwardsii* (*S. ciliatosepala*) and *S. laeta*, with scarious bract in the inflorescence and sepals that are ciliate-margined and densely soft-pubescent on the back, are known to me from a number of places in arctic Canada: Ellesmere Island, Lake Hazen, Harrington, No. 372; Baffin Island, Arctic Bay, Harrington, No. 467;

Thelon R., 64° 10′ N. and 102° 35′ W., E. Kuyt, No. 34. A *Stellaria* with pubescent sepals and scarious bracts known to Hultén from a few collections from interior Yukon and Alaska, he (l.c.) provisionally identified with the not too well understood *S. Laxmanni* Fisch., of central Siberia (*see* this later). In northern British Columbia, southwestern Yukon, and central Alaska there appears to be some evidence that such plants of heterogenous characters may be of very recent origin, occurring mainly in man-made environments, where they may represent crosses between introduced, weedy *S. longipes* (with glabrous sepals), *S. Edwardsii* (with ciliate sepals), *S. subvestita* (with glabrous sepals, scarious bracts, and pubescent internodes and leaves), and *S. laeta* (with pubescent sepals, but lacking scarious bracts).

During the winter of 1954–55, a visit to the herbaria of the British Museum of Natural History and Kew Botanic Gardens, London, enabled me to examine and photograph numerous sheets of North American and Asiatic *Stellaria* of the *longipes* complex, among them those on which Brown and Hooker based their original descriptions.[1] During a visit to the Komarov Botanical Institute, Leningrad, in 1957, I was able to examine Siberian members of the *Stellaria longipes* complex and to photograph the types of *S. peduncularis* Bge., *S. ciliatosepala* Trautv., *S. Laxmanni* Fisch., *S. florida* Fisch., and *S. falcata* Ser.[2]

In his revision, Hultén (l.c.), in addition to *S. longipes* Goldie, distinguished *S. crassipes* Hult., *S. laeta* Richards., *S. monantha* Hult., *S. ciliatosepala* Trautv. (the latter, as already surmised by Hultén, is antedated by the validly published *S. Edwardsii* R.Br.), and the doubtful *S. "Laxmanni."*

The conclusions reached by the present study are largely in agreement with Hultén's (l.c.) views that these taxa (excepting *S. "Laxmanni"*) represent distinct and in most cases workable geographical races. For the sake of clarity and convenience I should have preferred to treat them as geographical races of sub-specific rank, but in order not to add needlessly to their already complicated nomenclature, I shall, like Böcher (l.c.), leave the final decision to the future, when the taxonomy and genetics of members of this complex but very interesting group have been studied more fully and, preferably, on material grown under controlled conditions of light and temperature. Two other taxa treated by Hultén, l.c.—*S. ruscifolia* Pall, and the likewise clearly distinct *S. alaskana* Hult., the first of amphi-Beringian range, the second endemic to Alaska, as noted by him—do not belong in the *S. longipes* complex and, therefore, need not be considered here.

As being of equal rank with those mentioned above, I have, in the following key and taxonomic treatment, added *S. arenicola* Raup, *S. subvestita* Greene, and *S. stricta* Richards.

---

[1] This was made possible in part by a grant from the Penrose Fund of the American Philosophical Society.

[2] The visit to the Leningrad Herbarium, as well as subsequent visits to herbaria in Stockholm, Uppsala, Oslo, Trondheim, Copenhagen, Vienna, and Geneva, was made possible under a Fellowship of the John Simon Guggenheim Memorial Foundation.

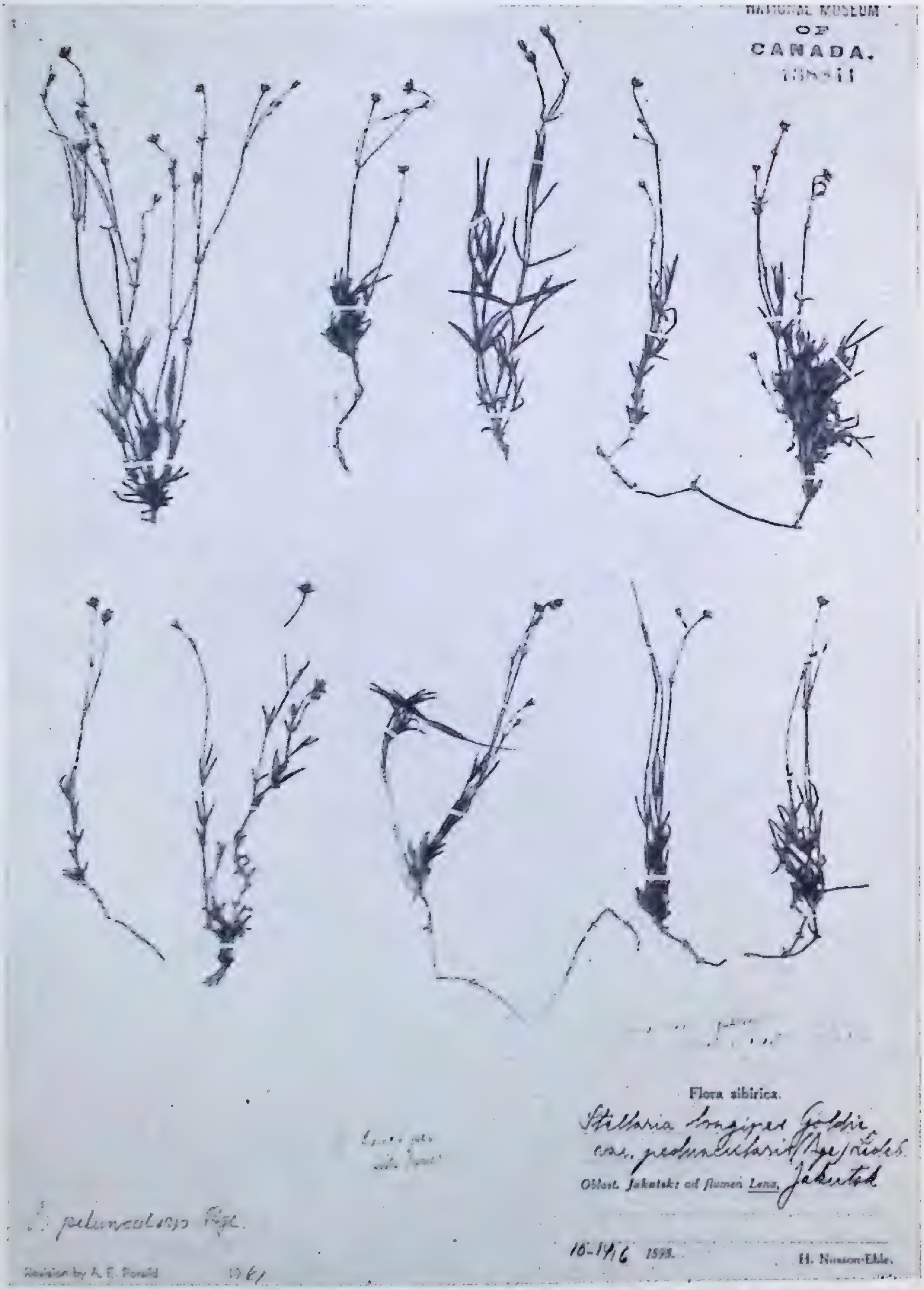
KEY TO NORTH AMERICAN MEMBERS OF THE *STELLARIA LONGIPES* COMPLEX

- A. Sepals entirely glabrous
  - B. Flowers in well-developed cymes, their peduncles supported by small scarious bracts; leaves commonly green and more or less shiny
    - C. Plant mostly high-grown
      - D. Stems and leaves glabrous or essentially so
        - E. Inflorescence with spreading branches, commonly rather few-flowered; flowers large, the petals much longer than the calyx
          - F. Capsule black and shiny, its valves not reflexed at maturity *S. longipes* s. str.
          - F. Capsule straw-coloured, its valves reflexed and rolled at maturity *S. arenicola*
        - E. Inflorescence many-flowered, with characteristically stiff and strongly ascending branches, the terminal flowers commonly approximate; petals scarcely longer than the calyx *S. stricta*
      - D. Stems strongly pubescent, especially on the internodes; leaves commonly villous, especially on the mid-rib dorsally and on the margins, rarely glabrate *S. subvestita*
    - C. Plants mainly of low and matted growth; flowers mostly solitary, pedicelled, in the axils of small, scarious bracts or scarious-margined green leaves; (rarely a second and lateral flower); capsules (very rarely present) pale with reflexed teeth *S. crassipes*
  - B. Flowers pedicelled, in the axils of normal green leaves, or if cymose with leaf-like bracts; leaves commonly bluish green *S. monantha*
- A. Sepals ciliated, glabrous or pubescent on the back
  - G. Flowers pedicelled, in few-flowered cymes, or solitary in the axils of scarious and mostly ciliated bracts
    - H. Sepals ciliated; internodes glabrous or sparingly pubescent *S. Edwardsii*
    - H. Sepals prominently pubescent on the back; internodes short-pubescent or villous; leaves villous, especially on the mid-rib and margins, rarely glabrate *S.* sp.
  - G. Flowers pedicelled, in the axils of normal green leaves; sepals normally pubescent on the back especially toward the tips, less commonly short-ciliate as well; plant fresh green and shiny *S. laeta*

Stellaria longipes Goldie in Edinb. Phil. J. 6: 327 (1822); Hooker, Fl. Bor.- Am., 1: 95 (1830); Hultén, Bot. Not. 1943, pro pte., excl. syn.; *idem* Fl. Al. & Yukon, pt. 4: 656 (1944) pro pte.; Böcher, Bot. Tidsskr. 48,4 (1951), pro pte.

Stellaria longipes Goldie appears to be the first member of this complex to have been formally recognized by botanists and, moreover, is one of the few among them about which there can be no doubt as to what plant was originally meant, because it is the only member of the group occurring in the type locality, and because Goldie clearly and adequately described the plants which he collected "in woods near Lake Ontario." The English version of his Latin diagnosis reads: "Stem long, filiform, square, and, as well as the whole, quite glabrous. Leaves narrow, linear-lanceolate, patent.

PLATE I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138841
Flora sibirica.
Stellaria longipes Goldie
var. peduncularis (Bge) Ledeb.
Oblast. Jakutsk: ad flumen Lena, Jakutsk
10-14/6 1898.
H. Nilsson-Ehle.
S. peduncularis Bge.
Revision by A. E. Porsild 1961

Stellaria peduncularis Bge. from Jakutsk, Lena R., Siberia, leg. H. Nilsson-Ehle (CAN 138841). Approx. half nat. size

Peduncles branched in a dichotomous manner; pedicels very long and slender, with two ovate acute bracteas, scariose in the margins. Flowers drooping before expansion. Calyx-leaves ovate, very obtuse, 3-nerved, margins scariose, scarcely shorter than the broad bipartite petals." Hooker's description (l.c.) is in close agreement with Goldie's, but adds: "Antherae fuscentes. Capsula ovato-oblonga, nigra, vel intense fusca, nitida, calycem paulo excedens, usque ad medium trivalvis, valvis raro bifidis."

By his opening statement: "Planta tota glaberrima," Hooker confirms one of the characters by which *S. longipes* s. str. is distinguished from some other taxa in this complex.

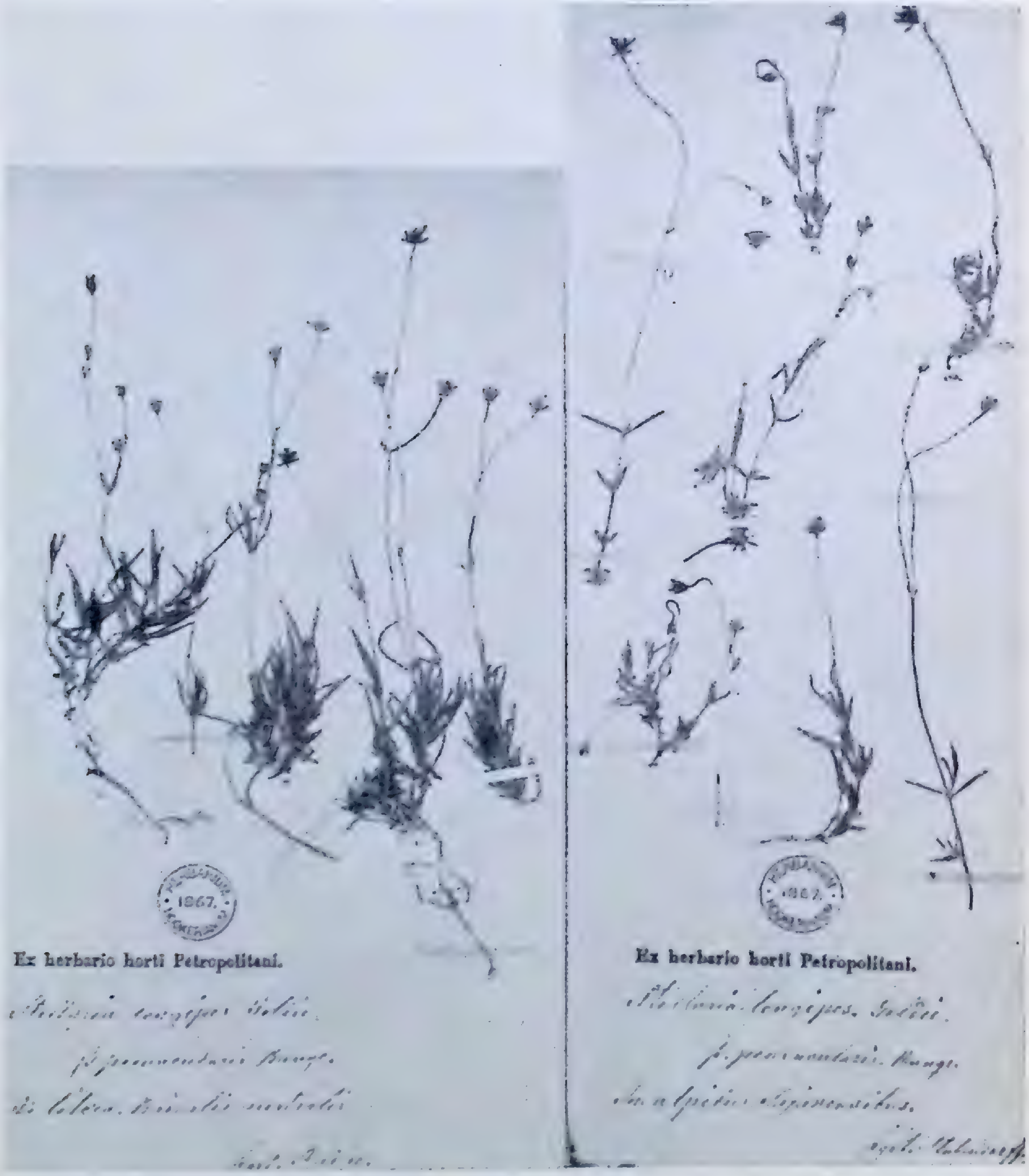
Although Fernald (in Gray's Man. ed. 8, p. 623) wrote "essentially glabrous," there can be little doubt that he, too, is dealing with *S. longipes* s. str., whereas Gleason (Illustr. Fl. vol. 2, pp. 126–7) clearly included other related taxa with his *S. longipes,* because he described the plant as "glabrous or somewhat pubescent." Furthermore, the plant he illustrated on page 127 completely lacks scarious bracts and obviously is *S. monantha* Hult.

Hultén (l.c.), under what he intended to be *S. longipes* s. str., included several elements that obviously do not fit *S. longipes* s. str. His statement that "the stem can be glabrous or sometimes slightly hairy" suggests that he may have included material of *S. subvestita* Greene, a taxon he knew only from the description, and which, elsewhere, he considered synonymous with *S. ciliatosepala* Trautv. Furthermore, under the synonymy of *S. longipes* Goldie, he included *S. stricta* Richards., *S. strictiflora* Rydb., *S. peduncularis* Bunge, and *S. nitida* Hooker, the latter described from the east coast of Greenland, where, according to his map (Hultén, fig. 22), no *S. longipes* s. str. occurs. In Asia, following a gap of over 3,000 km, between Bering Strait and the Lena River, Hultén's map shows a widely disjunct area extending through central and western Siberia west to Novaya Zemlya and Kolgujev. To the south of this area a black line, circumscribing the area of *S. longipes,* extends as a narrow corridor more than 2,000 km long, from the vicinity of Jakutsk over Lake Baical to somewhere in the Altai region. No dots are shown in this "corridor" which, apparently, was meant to include the type localities of *S. peduncularis* Bunge and, perhaps, *S. dahurica.* On phytogeographic grounds alone, the range assigned by Hultén to *S. longipes* s. str. is most unusual, and I cannot think of a single phanerogamic member of the North American boreal forest flora occupying a disjunct area in Eurasia such as the one shown by Hultén for *S. longipes* s. str. In justification of it, Hultén merely states that "The Asiatic material [presumably meaning *S. peduncularis* Bunge] can, however, hardly be separated from the American, as is proposed by Schischkin in Fl. S.S.S.R." *S. peduncularis,* however, has ciliate sepals as shown by the brief but very clear diagnosis in Ledeb. Fl. Alt., 2: 157 (1830), which reads: "St. caule tetragono erecto rigido parce piloso, foliis sublinearibus acutis margine laevibus glabris uninervis, peduncula terminali subdichotoma aphylla caule longiori, pedunculis longissimis glabris, petalis sepala lanceolata ciliolata superantibus bipartitis."

Among the Asiatic specimens cited by Hultén (l.c.), under *S. longipes* s. str., only one is available to me for comparison. This is CAN 138841, labelled *Stellaria longipes* Goldie var. *peduncularis* (Bge.) Ledeb., and is from Jakutsk on the Lena River, collected June 10–14, 1898, by H. Nilsson-

Ehle (Tab. I). This is a very slender plant with stems 10 to 15 cm long, including the long, naked peduncles; the internodes are sparingly pubescent, and the flowers are much smaller than in *S. longipes* Goldie, with narrow, acute, and ciliate sepals barely exceeded by the petals. It perfectly matches the description of *S. peduncularis* Bge. as well as the plant illustrated in

PLATE II


1867.
Ex herbario horti Petropolitani.
Ex herbario horti Petropolitani.

Stellaria peduncularis Bge. (*Left*): Lake Baical, Siberia, leg. Radde; (*Right*): Sajan Mts., Siberia, leg. Stubendorff; both from Herb. Hookerianum (K). Approx. half nat. size

Ledeb. Ic. Pl. Fl. Ross. Tab. 421, and also Tab. XXI, fig. 4 in Fl. S.S.S.R., vol. 6, and, incidentally, also Hultén's Fig. 1,e of *S. longipes* from "Siberia, Yenisei, Tolstoi Nos 1876 Brenner."

In Kew are a few sheets of *S. peduncularis.* Two collections, of which I made photographs, are labelled in the hand of Ledebour: "*Stellaria longipes* Goldie β *peduncularis* Bunge." The first "Ad litora Baicalis australis, legit Radde" and the second "In alpibus Sajanensibus, legit Stubendorff" (Plate II). Both are perfect matches for the Nilsson-Ehle collection.

When visiting the London herbaria in 1954–55, and the U.S.S.R. Academy of Sciences herbarium in Leningrad in 1957, I failed to discover specimens of *Stellaria* from the U.S.S.R. that could be satisfactorily referred to *S. longipes* Goldie, and I must, therefore, agree with the view expressed by B. Schischkin in Fl. S.S.S.R. that *S. longipes* Goldie does not occur in the Soviet Republic.

Hultén and Böcher (l.c.) agree that *S. longipes* s. str. is absent in East Greenland. With this view I am in full agreement, but I would even go a step further by questioning that it occurs in West Greenland. I, at any rate, have seen no typical *S. longipes* from Greenland, and I believe that all scarious-bracted plants, so named, from West Greenland are high-grown *S. crassipes* and that they will prove to have 2n=104 chromosomes as against 2n=52 reported for *S. longipes* Goldie in plants grown from seed obtained at Churchill, Man. (Böcher, l.c.).

Regardless of whether *S. longipes* s. str. occurs in West Greenland, it is obviously endemic to North America where its range strongly suggests that it is an eastern element in flora of the boreal forest region, extending from southern Labrador across Canada and northeastern United States, becoming progressively less common in the Northwest, where it does not reach the Pacific Coast (*see also* Porsild, 1958 and 1961). Although, as noted above, typical *S. longipes* is known from northern British Columbia and interior Yukon and Alaska, all such collections known to me are from embankments of recently constructed highways or railroads, airfields, and so forth, where they could well be recent introductions (*see* Figure 1 for total range of *S. longipes* s. str.).

Stellaria crassipes Hult. in Bot. Not. 1943, p. 261, fig. 1 h–n and map fig. 3, Böcher, Bot. Tidsskr. 48,4: 408 (1951), map 5; Porsild, Nat. Mus. Canada, Bull. 146: 75 (1957), fig. 29b and Map No. 132.

Hultén (l.c.) distinguished this taxon from *S. longipes* s. str. by its single or rarely two or more terminal flowers, supported by scarious-margined, reduced upper foliage leaves rather than by truly membranaceous, bract-like leaves, and by its thin and papery capsule with outward curved teeth. On page 263 it is said "In habit it is readily distinguished from *S. longipes* by the short sterile shoots in the axis of the upper leaves," a character which, however, is common to all members of the group and is particularly well developed under arctic and alpine conditions.

Were it not for its apparently distinctive geographic range, it would seem that *S. crassipes* could, at most, be considered a compressed, arctic-alpine form of *S. longipes,* as, indeed, it was until 1943 in Scandinavia, where it is the only member of the *S. longipes* group. In North America,

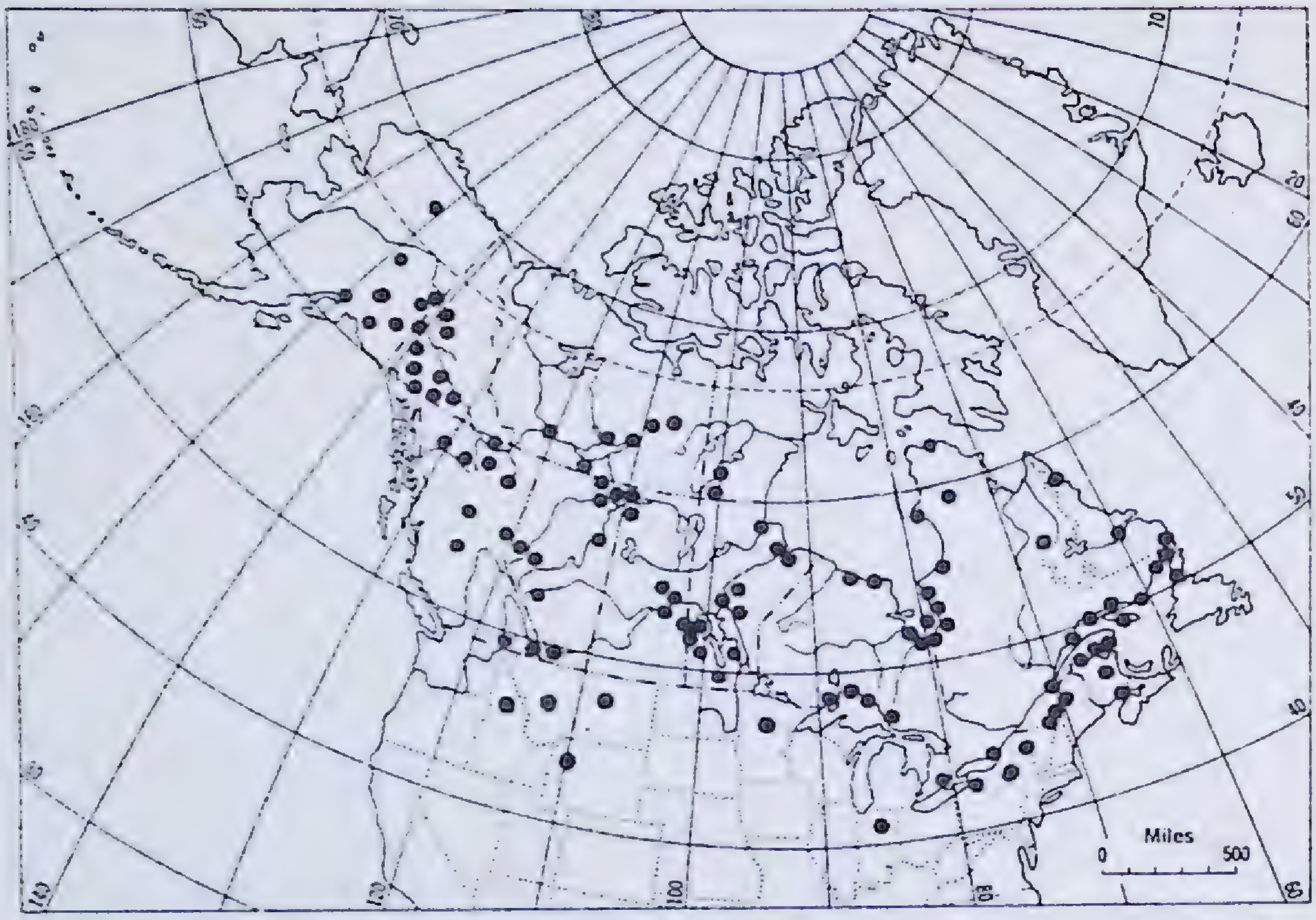


FIGURE 1. Total range of *Stellaria longipes* Goldie s. str.

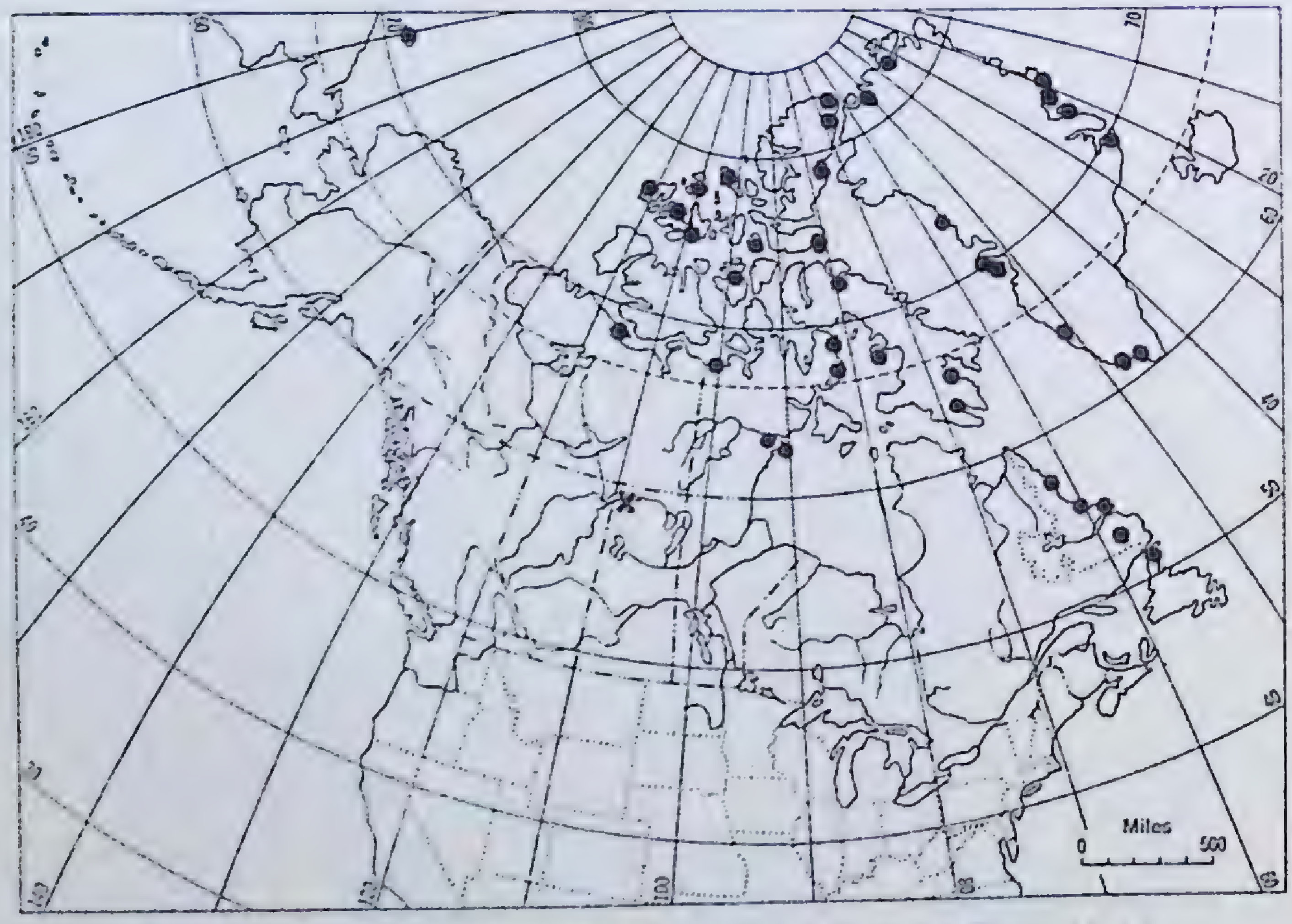


FIGURE 2. North American range of *Stellaria crassipes* Hult. (dots); total range of *Stellaria arenicola* Raup (cross)

on the other hand, where a number of races occur within this group, all of them variable in size and growth-form according to climate and habitat, it would seem very difficult, indeed, on morphological characters alone to separate dwarf forms of *S. longipes* s. str. from tall and high-grown plants of *S. crassipes*. It is inconceivable that such do not exist, even though it would seem impossible to prove except by the counting of chromosomes. As stated above, I have seen no *S. longipes* s. str. from Greenland where, I believe, the dots shown in Hultén's and Böcher's maps (l.c.) on the west coast actually indicate stations for a southern, and high-grown form of *S. crassipes* (*see* Porsild, 1957, Map No. 132). A similar situation exists in Eastern Canada where *S. crassipes* extends south to the Strait of Belle Isle and northern Newfoundland. In his latest map (1958, No. 7) Hultén included range extensions suggested for *S. crassipes* in the maps published by Böcher (l.c.) and myself (l.c.), with proper citation of source, although omitting, without comment, the additional southern stations shown on my map.

Although Hultén (l.c.) has described and illustrated the capsules of *S. crassipes* and obviously considered the characters by which they differ of taxonomic importance, it seems very doubtful if sexual reproduction actually occurs in this taxon. The capsules shown in Hultén's Fig. 1, m–n, certainly look abortive. Hartman, in Scand. Fl. 1879, p. 238, and Lindman, in Sv. Fan. Fl. 1926, p. 260, noted that fruits and seeds of "*S. longipes*" are not known from Scandinavia. More recently Söderberg (1954) noted that transplants of *S. crassipes* in the Bergius Botanical Garden, Stockholm, never produced fruits, whereas *S. longipes* grown from seed originating in Churchill, Man., and transplants of *S. monantha* from Ameralik, West Greenland, regularly produced abundant viable seeds. Asexual reproduction appears to be the rule in *S. crassipes* also in North America where, among the 30-odd specimens of North American *S. crassipes* before me, not one shows any indication that fruits may be, or were ever formed, not even in specimens collected late in the season in the southern limits of its range (*see* below).

Hultén (1958) considered *S. crassipes* amphi-Atlantic, and its North American range, as known at present, certainly favours this view. However, in the Herb. Bot. Acad., Leningrad, I saw a specimen labelled *S. Edwardsii* R. Br. collected on Wrangel Island, August 27, 1938, by B. Gorodkov. A duplicate of it is in the National Herbarium (CAN 240986). It is densely pulvinate, and in growth-form entirely matches the description of *S. arctica* Schischkin (Fl. S.S.S.R. vi, p. 881, 1936, by Hultén (1943) reduced to *S. ciliatosepala* var. *arctica*), except that the Gorodkov plant is totally glabrous, even to the feebly developed scarious bracts and to the sepals of the small, solitary flowers in beginning anthesis. A duplicate of yet another specimen, likewise labelled *S. Edwardsii* R. Br., but closely matching the Wrangel Island plant, was recently received from Leningrad (CAN 265304). It was collected in the Franz-Josef Archipelago, on Alexandra Land, Aug. 10, 1959, by V. D. Alexandrova. It is part of a densely tufted mass of stems covered by the marcescent leaves of past seasons, each stem terminated by one or two pairs of green leaves, a few of them enclosing unexpanded flower buds. In the axils of the upper marcescent leaves are green axillary buds, and on several stems, apparently killed by early frost the preceding year, are the remains of undeveloped flowers, supported by scarious bracts. No trace of pubescence or ciliae can be detected on the bracts, or on the sepals of the new flower buds. Both collections clearly are *S. crassipes*. The Alexandrova specimen confirms Böcher's report of *S. crassipes* (l.c., p. 409) from Cape Forbes and, together with the new and widely disjunct Wrangel Island station, suggests that the range of this taxon may be circumpolar rather than amphi-Atlantic. The following, hitherto unpublished records from mainly non-arctic North American stations of *S. crassipes*, are in the National Herbarium of Canada:

West Greenland: Neria, lat. 61° 33′ N., July 18, 1929, J. Eugenius; Kingua Tasiusak, lat. 61° 45′ N., N. Hartz an. 1889; Itivneq ved Ameralikfjorden, c. 64° 20′ N., July 26, 1913, J. N. Nygaard; Disko, Godhavn, July 25, 1936, Aa. Jensen.

Labrador: west bank of Hamilton River, July 13, 1894, A. P. Low; sandy shore of Rigolet, July 17, 1921, R. H. Wetmore; Indian Harbour, lat. 54° 25′ N., H. Bishop 298.

Quebec: Mollie T. Lake, lat. 55° 03′ N., long. 67° 10′ W., Aug. 13, 1953, F. Harper 3821.

Newfoundland: Cook Harbour, lat. 51° 33′ N., long. 55° 33′ W., July 31, 1949, Tuomikoski 228.

These, and some new western and northern arctic stations, are shown on map fig. 2, giving the North American range of *S. crassipes*.

Stellaria arenicola Raup in J. Arn. Arb. 17: 248, pl. 196 (1936).

As noted by Raup (l.c.) *S. arenicola* in habit and general appearance is very similar to *S. longipes* Goldie, s. str., but differs from it mainly in having straw-coloured capsules with reflexed and rolled valves in the mature condition. Duplicates of the type (Raup, 6882) and paratypes (Raup, 6883 and 6910) are in the National Herbarium of Canada. By its pale, straw-coloured stem, remarkably long and perfectly glabrous internodes, and by its freely branching and rich-flowered inflorescence and short, pale capsules, *S. arenicola* exhibits a rather striking contrast to *S. stricta* Richards. and *S. longipes* Goldie, but in view of the scarcity of material, it would, perhaps, be hazardous to attach too much significance to these differences. Number 6910 is that of a fruiting plant; the inflorescence is more condensed than in the type. Most of the dehizing capsules appear normal, and several still contain a few, seemingly normal and fully-developed seeds.

Thus far, *S. arenicola* is known only from the type locality, on sand dunes south of William Point, on the south shore of Athabasca Lake in N.W. Saskatchewan, a local area noted for its remarkable concentrations of endemics. William Point and vicinity is the type locality of no less than ten taxa, of which all but the last two appear to be endemic to the area: *Salix brachycarpa* var. *psammophila* Raup; *S. Tyrrellii* Raup, *S. Turnori* Raup, *S. silicicola* Raup, *Alnus crispa* var. *elongata* Raup, *Stellaria arenicola* Raup, *Statice interior* Raup, *Achillea megacephala* Raup, *Tanacetum huronense* var. *floccosum* Raup, *Cicuta mackenzieana* Raup, and *Deschampsia mackenzieana* Raup.

The description and the excellent figure accompanying *S. arenicola* appear to have escaped both Hultén (1943) and Böcher (1951). The location of the type locality is marked by a cross in map fig. 2.

Stellaria stricta Richards. [*β* caulibus glabris] in Hook., Fl. Bor.-Am. 1: 96 (1830); Rydberg, Fl. Prairies and Plains of Centr. N. Am. 1932, p. 317, fig. 201.

S. palustris α Richardson in Frankl. 1st. Journ. ed. 1, App. vii, p. 738 (1823) non Retz.

Alsine strictiflora Rydb. Bull. Torr. Bot. Cl. 39: 315 (1912).

Although Hooker (l.c.) reversed the varietal designations α and β, there can be no doubt as regards to which plant Richardson applied the epithet *"stricta,"* for of the var. β of Richardson (l.c. 1823) was said "differt tantum habitu strictiori, caule villoso et foliis non glaucis" which clearly refers to the taxon now known as *S. subvestita* Greene, Ott. Nat., 15: 42 (1901), whereas Hooker's opening statement "stricta nitidissima" could only have meant *S. stricta.*

An examination of Richardson's specimens fully confirms this. As no lectotype has been designated, I propose for this a specimen from Herb. Benthamianum, now at Kew, collected by Richardson on Great Bear Lake, and in the hand of Hooker labelled *"Stellaria stricta β"* bearing a printed label below the specimen reading "North American Hooker, 1835" (Plate III). A second specimen, this from Herb. Hookerianum, likewise labelled *"Stellaria stricta β,"* was collected at York Factory by Drummond (Plate IV). Both are perfectly glabrous plants with the characteristically "strict" habit noted by Richardson.

S. stricta is closely related to *S. longipes* and *S. arenicola* Raup and, like these, is perfectly glabrous and highgrown, differing by its narrower and more rich-flowered inflorescence in which the branches are strongly ascending and the terminal flowers often approximate; the bracts are membranaceous and entirely glabrous; the flowers are smaller, with sepals about 5 mm long and petals not much longer than the glabrous sepals; the black and shiny mature capsules are about one-third longer than the calyx; sexual reproduction appears to be normal and regular.

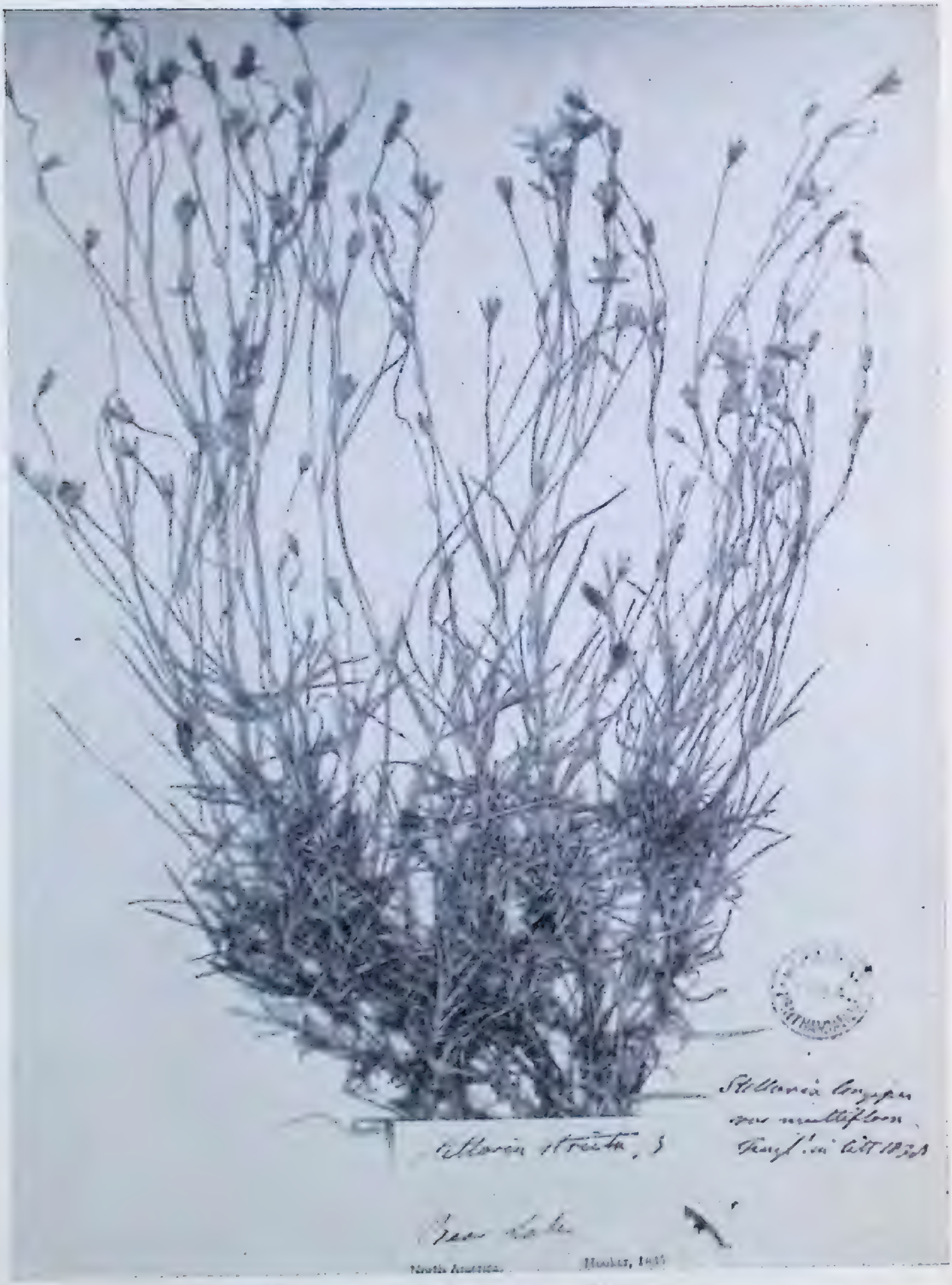
S. stricta is a prairie and foothills species commonly growing in damp meadows and on sandy river banks and lake shores, from James Bay and western Ontario west to Alberta and interior British Columbia, north to S.W. Yukon and central and upper Mackenzie District (with one widely disjunct station in the Mackenzie Delta), south in the western United States to Colorado and California.

The following specimens in the National Herbarium of Canada are representative:

ONTARIO: N. shore Lake Superior, Port Arthur, W. H. Harrington, CAN 99118; Thunder Bay, long. 86° 15′ W., T. M. C. Taylor 287; Fort Severn, lat. 56° N., long. 87° 30′ W., Hustich 1406.

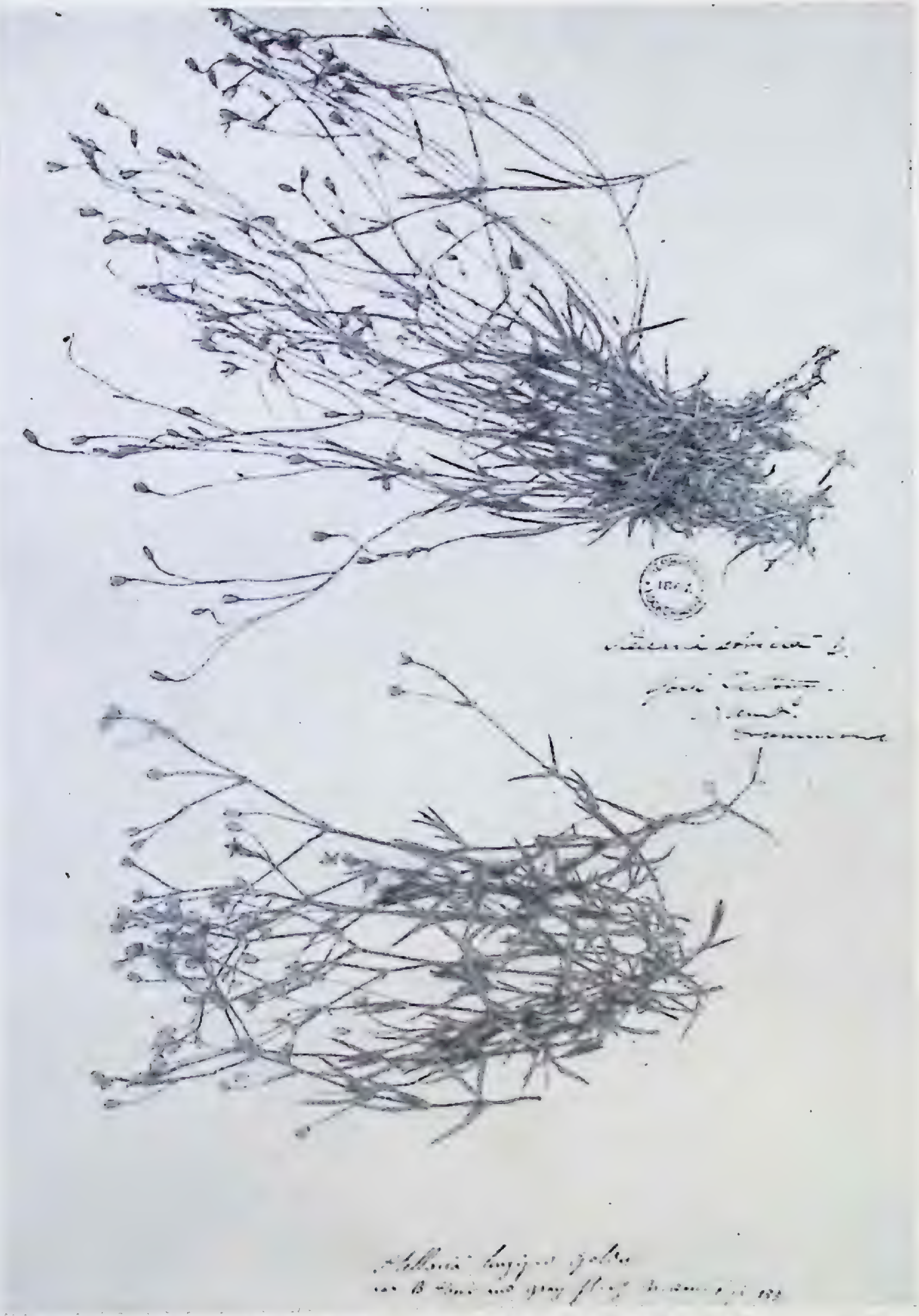
JAMES BAY: Goose Bay, Que., Baldwin, etc., 680; Kinoshayo Pt., lat. 52° 10′ N., long. 81° 27′ W., R. H. Smith, 22.

MANITOBA: Churchill, Mosquito Pt., Porsild 5530; G. Gardner 25a; Carberry, W. Herriot CAN 70910; Portage la Prairie, *idem* 70909; Mac-



Lectotype of *Stellaria stricta* Richards.
From Great Bear Lake, N.W.T., Canada, leg. J. Richardson. From Herb. Benthamianum (K). Slightly more than half nat. size

PLATE IV



Stellaria stricta Richards. from York Factory, Manitoba, Canada, leg. Drummond. From Herb. Hookerianum (K). Approx. half nat. size

Gregor, *idem,* CAN 70908; Winnipeg, River Pk., Macoun CAN 12454; Stonewall, Macoun CAN 12453; Brandon, Dauphin, Scoggan 7551; Norway House, Scoggan 2537; Macoun CAN 12465; York Factory, Drummond (K).

SASKATCHEWAN: Prince Albert, Macoun CAN 12462; Moose Jaw, Macoun CAN 12441; Swift Current, Macoun CAN 4010; Farewell Creek, Macoun CAN 10130; Cypress Hills, J. M. Macoun CAN 4739; Redpath, Herriot CAN 70907.

ALBERTA: MacAllister n. of Dunvegan, J. M. Macoun CAN 59573; Cardston, Macoun CAN 10128; Ft. Saskatchewan, Geo. Turner 6133; Morley, Macoun CAN 4726 and 4731; Jumping Pound Creek, Macoun CAN 18229; Jasper Park, H. M. Laing 265; Upper Red River, Ya-ha-tinda Ranch, Porsild 18243.

BRITISH COLUMBIA: Summit Lake, J. A. Munro 108; Elk River north of Natal, W. A. Weber 2390; Prince George, J. W. Eastham 11643; MacLeod Lake, Macoun CAN 4725; Alaska Highway, Minaker River, C.H.D. Clarke 17; Vancouver Island, Sidney, Macoun CAN 86830.

NORTHWEST TERRITORIES: Liard River between Nahanni Butte and Simpson, C. H. Crickmay 37; Great Bear Lake, Richardson (K); Arctic Coast, Tuktoyaktuk, Porsild 7417a. Steep, wooded bank above Simpson, Porsild 16589; Ft. Providence, Lindsay 171.

YUKON TERRITORY: Johnson Crossing, Porsild 18406; Makintosh, Schofield & Crum 7517.

IDAHO: N.W. of Kilgore, Bassett Maguire 17168.

MONTANA: Big Hole River, 6 mi. north of Wisdom, Hitchcock & Muhlick 12588.

COLORADO: Leadville, Sept. 7, 1886, Trelease.

CALIFORNIA: Bear Valley, San Bernardino Mts., 6500 ft., S. B. Parish 3346. For total range see map fig. 3.

Stellaria subvestita Greene in Ott. Nat., 15: 42 (1901).

S. palustris var. *β.* "*. . habitu strictiori, caule villoso et foliis non glaucis*" Richardson in Frankl. 1st Journ., ed. 1, App. vii, p. 738 (1823).

S. stricta var. *a* "*caulibus laxe pubescenti-pilosis*" Hooker, Fl. Bor.-Am. 1: 96 (1830).

S. longipes var. *subvestita* (Greene) Polunin, Nat. Mus. Canada, Bull. 92: 192 (1940).

Alsine subvestita (Greene) Rydb. Fl. Rocky Mts., p. 270 (1917).

Stellaria subvestita has the general habit of *S. longipes* Goldie s. str., from which it differs by its green, non-glaucous, pilose to glabrate, narrower and more attenuate leaves and always pubescent internodes. The capsules are black and shiny, slightly shorter than in *S. longipes,* and the petals but slightly longer than the glabrous sepals. Greene (l.c.) stated that the nerve of the sepals is "often pilose" and that the bracts of the cyme are

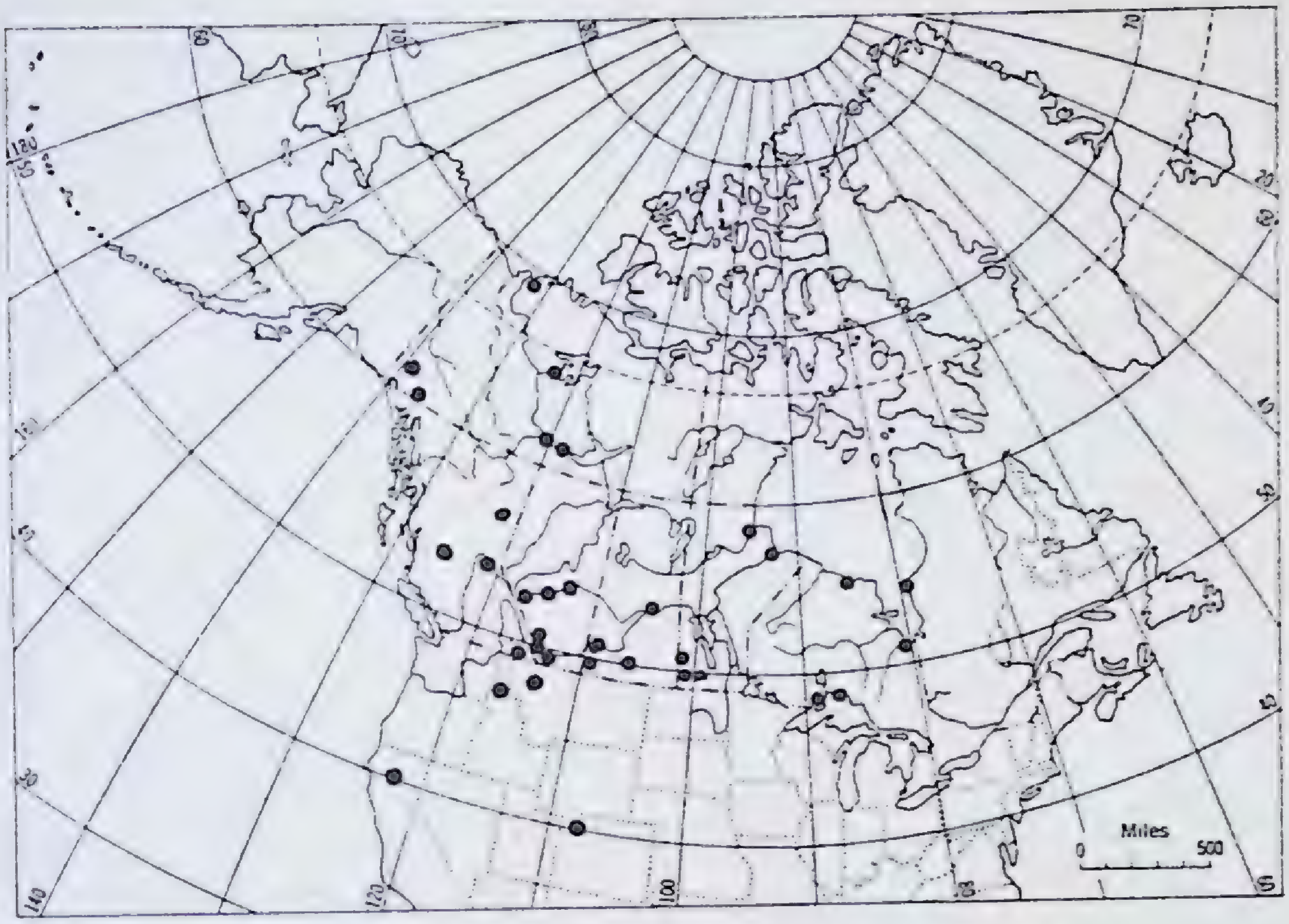


FIGURE 3. Total range of *Stellaria stricta* Richards.

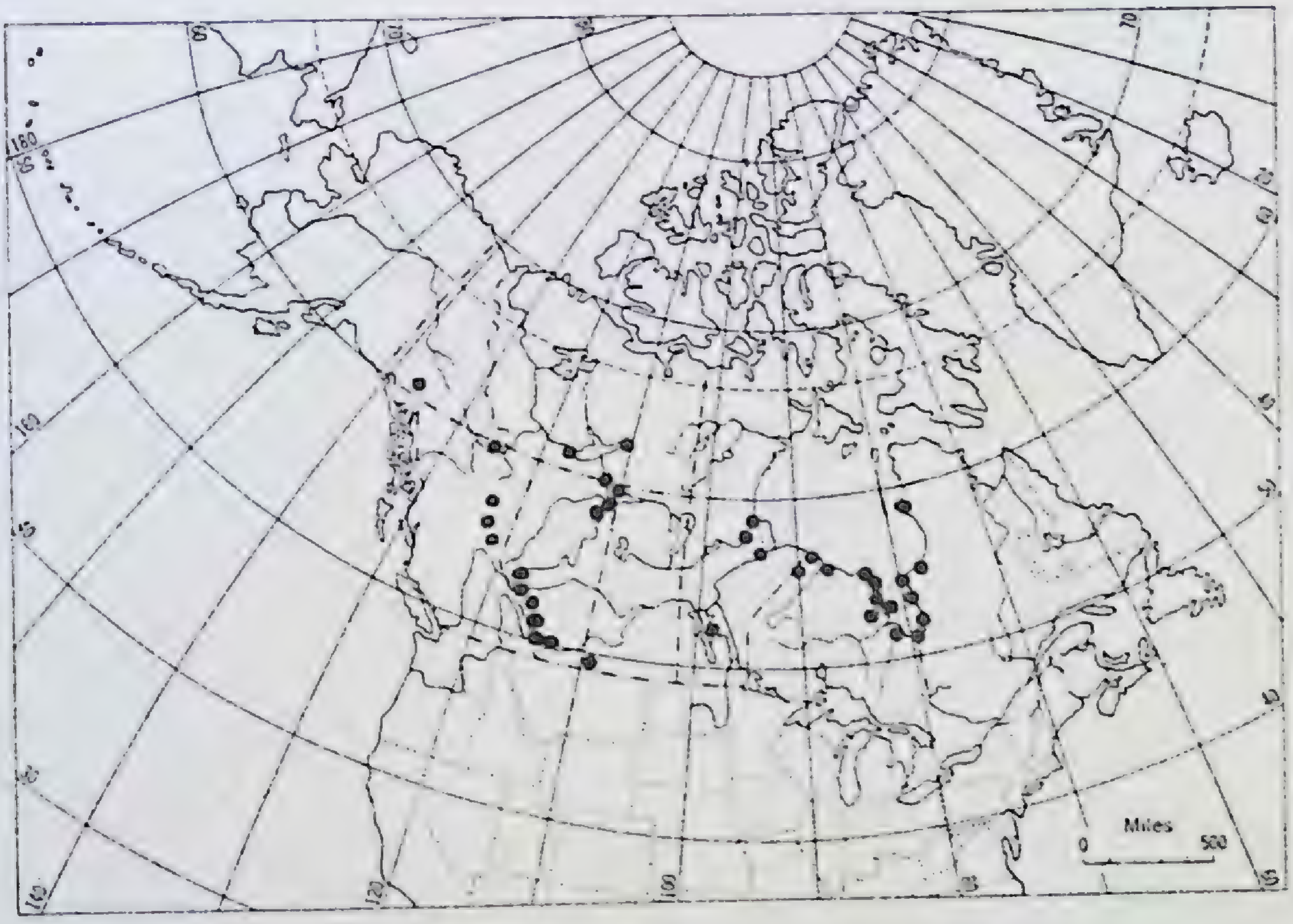


FIGURE 4. Total range of *Stellaria subvestita* Greene

"often villous-ciliate." In the abundant material before me, a few ciliae are often present near the base of the scarious bracts of the inflorescence, but in only one flower of the lectotype have I been able to detect a trace of pubescence on the sepals.

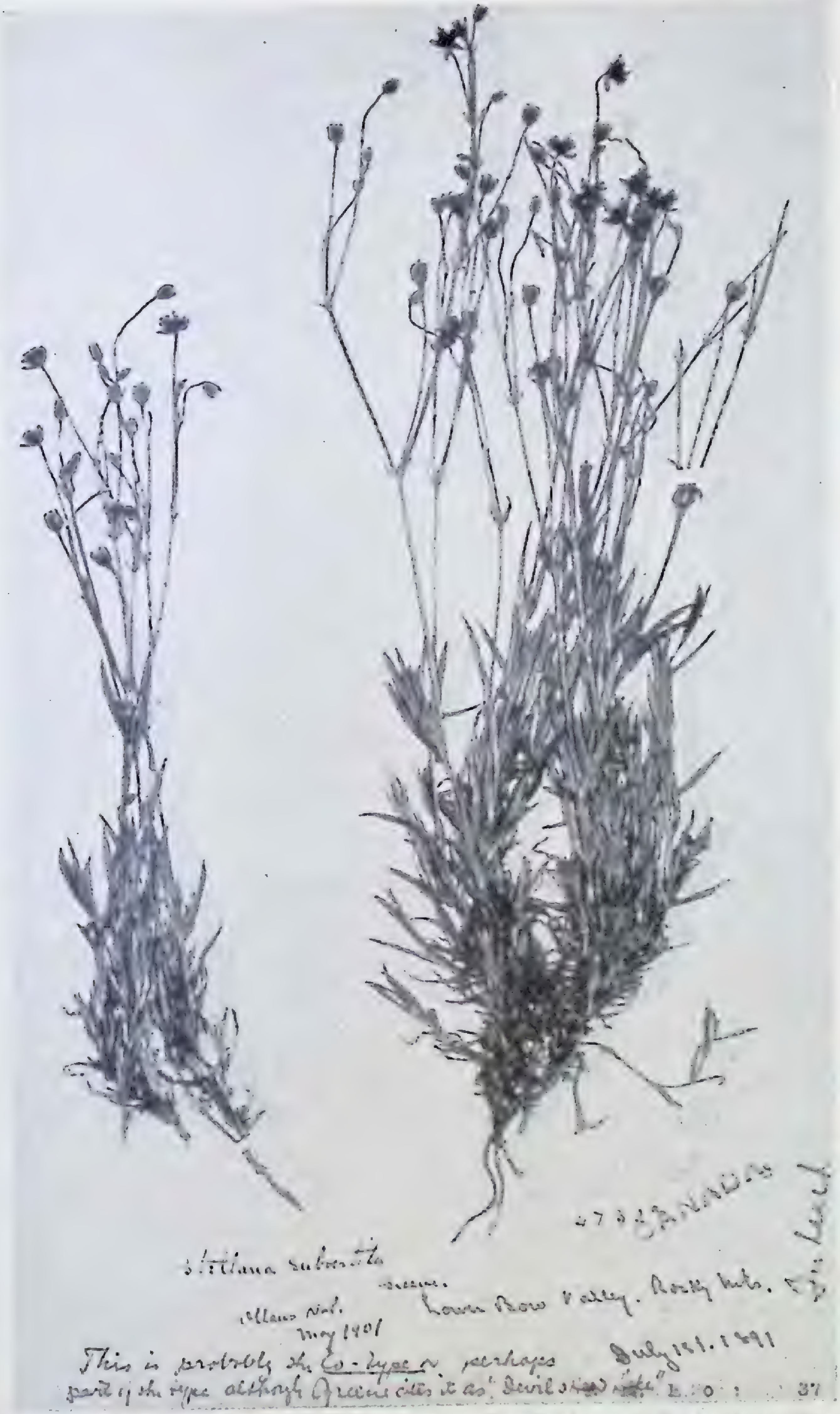
Hultén (l.c., p. 261) concluded from Greene's description that *S. subvestita* is conspecific with *S. ciliatosepala* [*S. Edwardsii*]. As will be seen from the discussion above, this clearly is not the case.

S. subvestita is a prairie and foothill species, commonly growing in well-drained, grassy, rather dry places, with a general range rather similar to that of *S. stricta*, but not known to me from south of the United States border. In Banff and Jasper National Parks it is very common in the subalpine zone well below timberline where it is the only common member of the *S. longipes* group.

Greene (l.c.) cited only two collections of *S. subvestita*: "Devil's Head Lake [Lake Minnewanka], and Banff National Park, July, 1891. Prof. John Macoun." No duplicate of the first-cited specimen has been retained in the National Collection; a duplicate of the second (Plate V), here selected as the lectotype, is CAN 51388, and is labelled "*Stellaria subvestita* Greene, Ott. Nat. May 1901" in the hand of John Macoun, and "Lower Bow Valley, Rocky Mts. July 1, 1891," by J. M. Macoun. For total range see map fig. 4.

Stellaria monantha Hult., in Bot. Not. 1943, p. 265, fig. 7 a–f; *idem* Fl. Al. & Yukon, pt. 4: 658 (1944); Böcher Bot. Tidsskr. 48, 4: 405 (1951), map fig. 1 B.; Porsild, Nat. Mus. Canada, Bull. 146: 75 (1957), fig. 29 g, and Map No. 133.

Stellaria monantha is distinguished from *S. crassipes, S. stricta, S. subvestita*, and from dwarf forms of *S. longpipes*, s. str., by the absence of scarious bracts or scarious-margined, reduced leaves in the inflorescence, and from *S. laeta, S. Edwardsii,* and from *S. "Laxmanni"* sensu Hultén, by its glabrous and non-ciliate sepals. The type: S. E. Alaska, Glacier Bay, June 13, 1899, leg. Kincaid, is in Stockholm, and a duplicate of the type is at Kew. In its typical form *S. monantha* is a densely matted or tufted plant, in habit resembling *S. laeta,* and within the range of *S. crassipes* not always distinguishable from dwarf forms of that taxon. The entire plant is normally glabrous although sometimes the internodes may be pruinose or bearing a few, short hairs; in the living state the entire plant is often, and perhaps normally, glaucous, so much so that a mat of *S. monantha* often appears distinctly bluish. Like other members of the *S. longipes* complex, *S. monantha* is well equipped for vegetative reproduction by its well-developed, creeping underground stems and by the production of wintergreen axillary buds. Although it flowers abundantly and is known to produce viable seeds, fully mature capsules are but rarely found, even under subarctic conditions. M. P. Porsild (1920) when observing that *S. longipes,* on Disko on the west coast of Greenland, is "abundantly flowering but very seldom fruiting," undoubtedly referred to *S. monantha,* which is by far the most common representative of *S. longipes* s. lat. on Disko. The fact that *S. monantha* (as indeed other members of the group) is late-flowering, may well account for the scarceness of ripe


CANADA
Stellaria subvestita
Greene.
Lower Bow Valley. Rocky Mts.
May 1901
This is probably the co-type or perhaps
part of the type although Greene cites it as "Devil's Head Lake"
July 1st. 1891
37

Lectotype of *Stellaria subvestita* Greene from Banff National Park, Alta., Canada (CAN 51388). Slightly more than half nat. size fruits under arctic conditions, for Söderberg (1954) reported abundant seed production in plants grown in Sweden, from transplants obtained in West Greenland.

As in other members of the *S. longipes* complex, *S. monantha* in lowland stations and in the southern parts of its range, naturally is taller and better developed than when grown in the Arctic. Such non-arctic plants, by Hultén (*see* his fig. 7 *a* and *b*) have been separated into a North American Atlantic race; ssp. *atlantica*, distinguished from *S. monantha* by: "*partibus omnibus majoribus valde glaucis; caulibus 10–15 cm altis; foliis c. 2 cm longis c. 3 mm latis planis; pedunculis 5–8 cm longis; floribus majoribus solitariis hemisphaericis; capsulis subglobosis calyce fere aequilongis.*"

When a larger material than Hultén had at his disposal is examined, it at once becomes clear that, on the basis of the above statement, no sharp line can be drawn between typical *S. monantha* and the ssp. *atlantica*. The western var. *altocaulis* (Hultén, fig. 7 *c* and *d*), known to him only from four widely disjunct stations from Alaska to Colorado, is distinguished by "*partibus omnibus majoribus; caulibus 10–15 cm altis interdum ramosis 1–3 floriferis; foliis caulinis omnibus lanceolatis.*" Surely but slight significance can be attributed to these characters that may be found in plants grown in sheltered subalpine forest anywhere within the range of *S. monantha* that, under such conditions, may attain a height of 20 cm, or more.[1] A parallel woodland form of *S. Edwardsii* is common in interior Alaska and Yukon, where specimens measuring 30 cm in height occur. Hultén (l.c., p. 268) writes that his var. *altocaulis* "might be suspected of being the *S. strictiflora* of Rydberg . . . but his picture (fig. 201) of '*S. laeta*' in his Fl. Prairies and Plains Centr. N. Amer., p. 317, which he there says is a synonym of his *S. strictiflora*, shows the *Stellaria longipes* type from the Rocky Mts. and not our plant." Hultén, somehow, misunderstood this passage, for Rydberg's fig. 201 clearly illustrates *S. stricta* Richards. (not *S. laeta*), for which the correct synonym, *S. strictiflora*, is given, and it could not possibly have been intended for *S. laeta* which Rydberg treated as a separate taxon, on page 318.

S. monantha, in common with *S. laeta*, is North American and mainly of arctic and subarctic range; perhaps slightly less arctic than *S. laeta*, although a glance at the maps (Figures 5 and 6) shows that both reach the northern tip of Ellesmere Island. Neither taxon has been reported from East Greenland; in the Bering Strait region both, according to Hultén (l.c. maps 8 and 9), reach the Chuckchi Peninsula.

Böcher (l.c.) who believes it low-arctic, noted that in Greenland no *S. monantha* has been collected north of the Upernavik region (lat. 72° 40′ N.) For this reason he suggests that a flowering specimen of *S. monantha* in the Copenhagen herbarium "from Grant Land 82° 30′ May 11, 1910, MacGregor," must have been collected in a more southern latitude. However, an examination of the original "MacGregor plant" in the herbarium at Kew shows that Capt. Bartlett (the skipper of Peary's ship *Roosevelt*) collected this plant, and that Sir W. MacGregor presented the specimen to Kew on May 11, 1910. No date of collection is given, but inasmuch as the *Roosevelt* left her winter quarters near Cape Sheridan on the N.E. coast of what is now officially known as Ellesmere Island, on July 18, 1909, Bartlett likely made the collection near his winter quarters in the early part of July of that year. More recent proof that *S. monantha* grows in northern Ellesmere Island is found in three recent collections now before me (lat. 83° N., long. 76° W., Hattersley-Smith, Nos. 55 and 56; near Alert, lat. 82° 21′ N., S. MacDonald, No. 24). All are as well developed as the Bartlett specimens, and with fully expanded flowers, in the last week of July.

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[1] No types for ssp. *atlantica* or var. *altocaulis* were designed by Hultén. Presumably the plants illustrated in his Figure 7 may be considered the types.

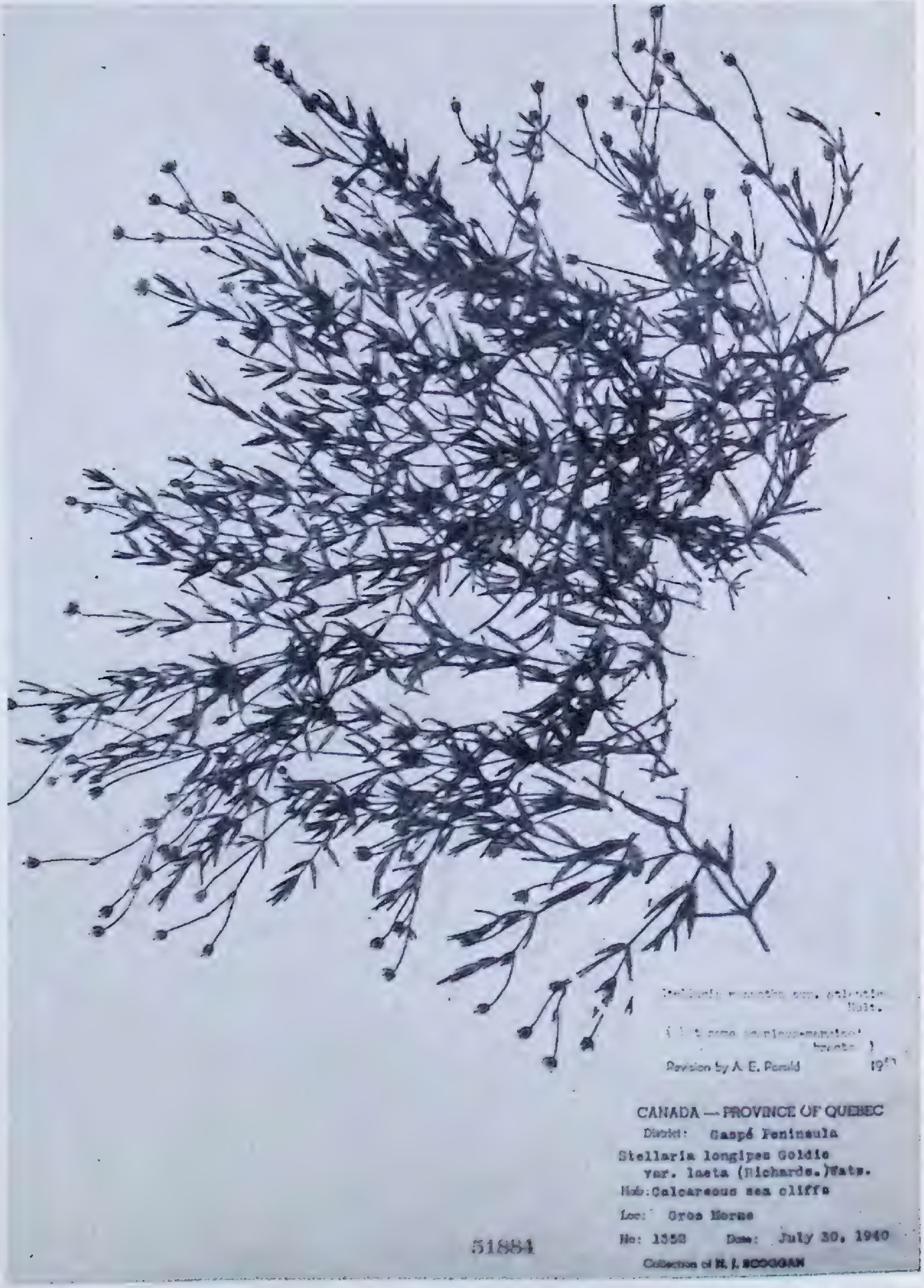
S. monantha, as well as *S. laeta,* in common with a rather large number of North American (or circumpolar) arctic plants, is found in alpine situations, more or less disjunct from its main range, in the Rocky Mountains. In the East it reaches the Gulf of St. Lawrence, and on sea-cliffs at Gros Morne on Gaspé it is represented by a tall-grown, 20 cm tall, much-branched, and rich-flowered plant exactly matching *S. longipes* s. str., except that it entirely lacks scarious bracts in the inflorescence (Pl. Exsicc. Gray. No. 549. *Stellaria longipes* Goldie, and also H. J. Scoggan, No. 1352, the latter distributed as *S. longipes* var. *laeta*). In the last-mentioned, a few, and the smallest, of the otherwise foliaceous bracts in the inflorescence are feebly scarious-margined, and it could, therefore, be referred equally well to *S. crassipes.* The Scoggan specimens, on July 30, are barely past flowering (Plate VI).

In the rather abundant material in the London herbaria, of *S. longipes* s. lat., contributed by the early British expeditions to North America, there are several collections of *S. monantha.* All, however, are mounted together with, or appearing as mixtures in, collections of *S. Edwardsii, S. stricta, S. laeta,* or *S. longipes* s. str., where they may well represent some of the "intermediate states" that Hooker (l.c.) confessed inability satisfactorily to refer to either of the taxa listed by him. At any rate, there is no indication in the writings of either Brown, Richardson, or Hooker, or in the annotations of specimens made by them on the sheets in the herbaria of the British Museum (Natural History) or Kew Gardens, that they had recognized or attempted to separate *S. monantha* from the very similar *S. laeta.* For total range see map fig. 5.

Stellaria laeta Richards. in Frankl. Narr. Journ. Polar Sea, App. vii, p. 738 (1823); Hooker, Fl. Bor.-Am. 1: 96 (1830); Hultén, Bot. Not. 1943, p. 264, fig. 7 g–h and map fig. 8; *idem,* Fl. Al. and Yukon, part 4: 654 (1944); Böcher, Bot. Tidsskr., 48,4: 413 (1951), map fig. 4; Porsild, Nat. Mus. Canada, Bull. 146: 75, fig. 29,d and map fig. 135 (1957).

In the British Museum (Natural History) is a sheet stamped "British North America. Dr. Richardson 1819–22" on which are mounted four plants that are completely glabrous except for the sepals that are ciliate and thinly pubescent on the back. On three of the plants there are from one to four single flowers; the fourth is a mere scrap and lacks flowers altogether. The plants are low and have developed from shiny, white subterranean stems suggesting that the four specimens once were part of a loose mat or cushion. A small label pasted below the specimens is marked "*Stell. laeta,*" and a larger one, below the first, reads "*Stellaria laeta* Richardson!" The handwriting on the first label clearly is that of

PLATE VI


Hult.
Revision by A. E. Porsild
CANADA — PROVINCE OF QUEBEC
District: Gaspé Peninsula
Stellaria longipes Goldie
var. laeta (Richards.)Wats.
Hab:Calcareous sea cliffs
Loc: Gros Morne
No: 1353 Date: July 30, 1940
Collection of H. J. SCOGGAN
51884

Stellaria monantha Hult. from Gaspé, Que., Canada (CAN 51884). Approx. half nat. size

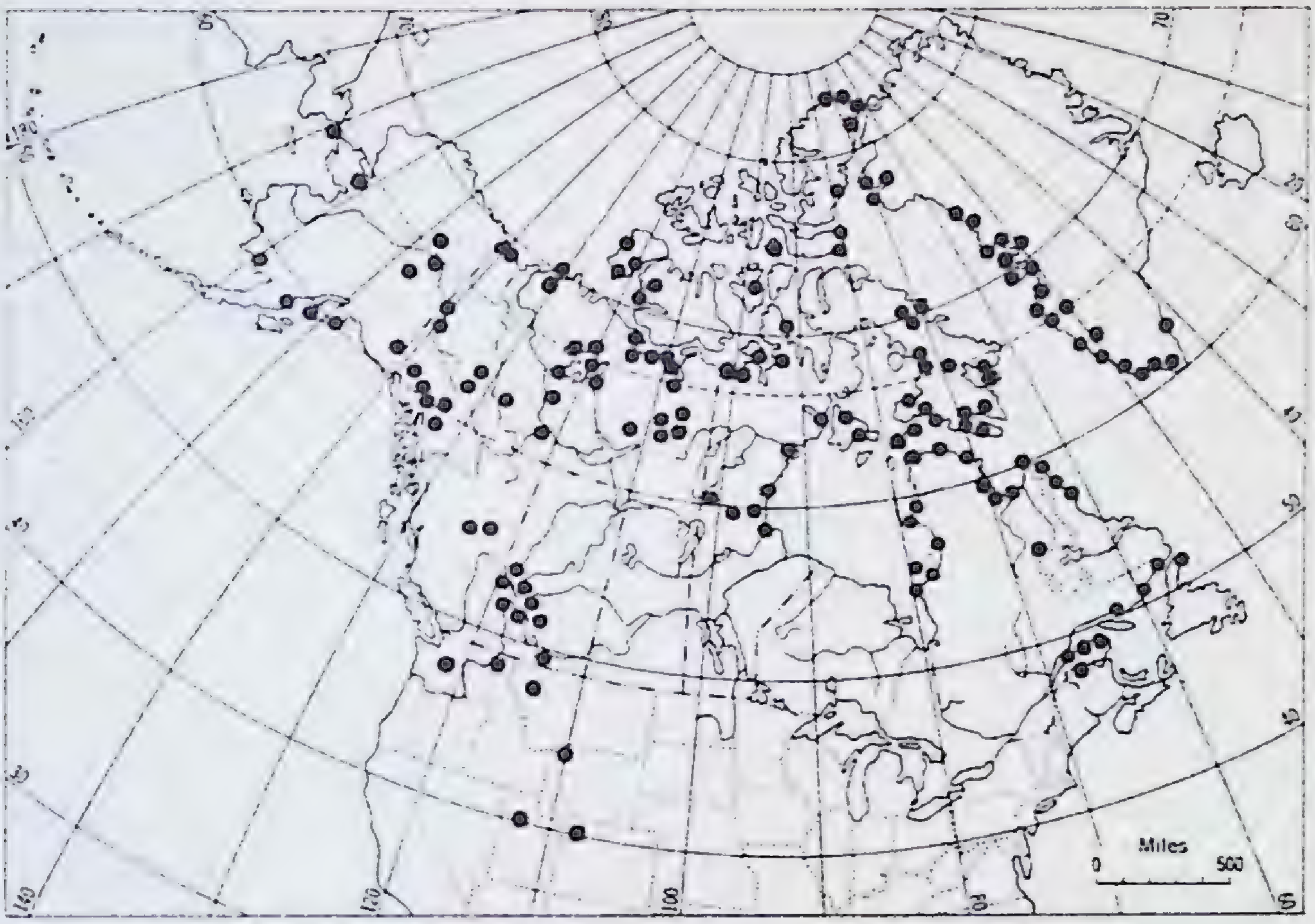


FIGURE 5. Total range of *Stellaria monantha* Hult.

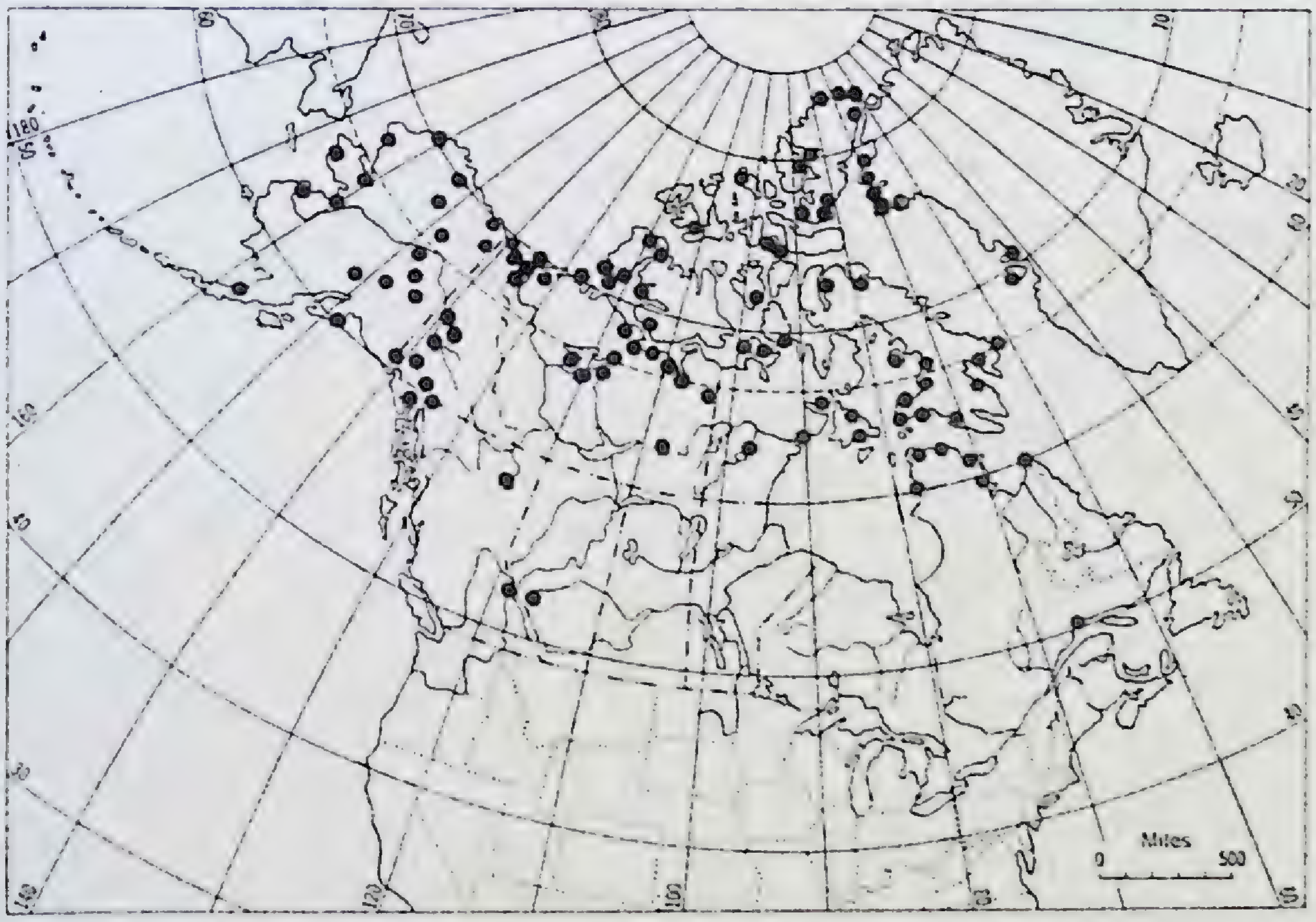
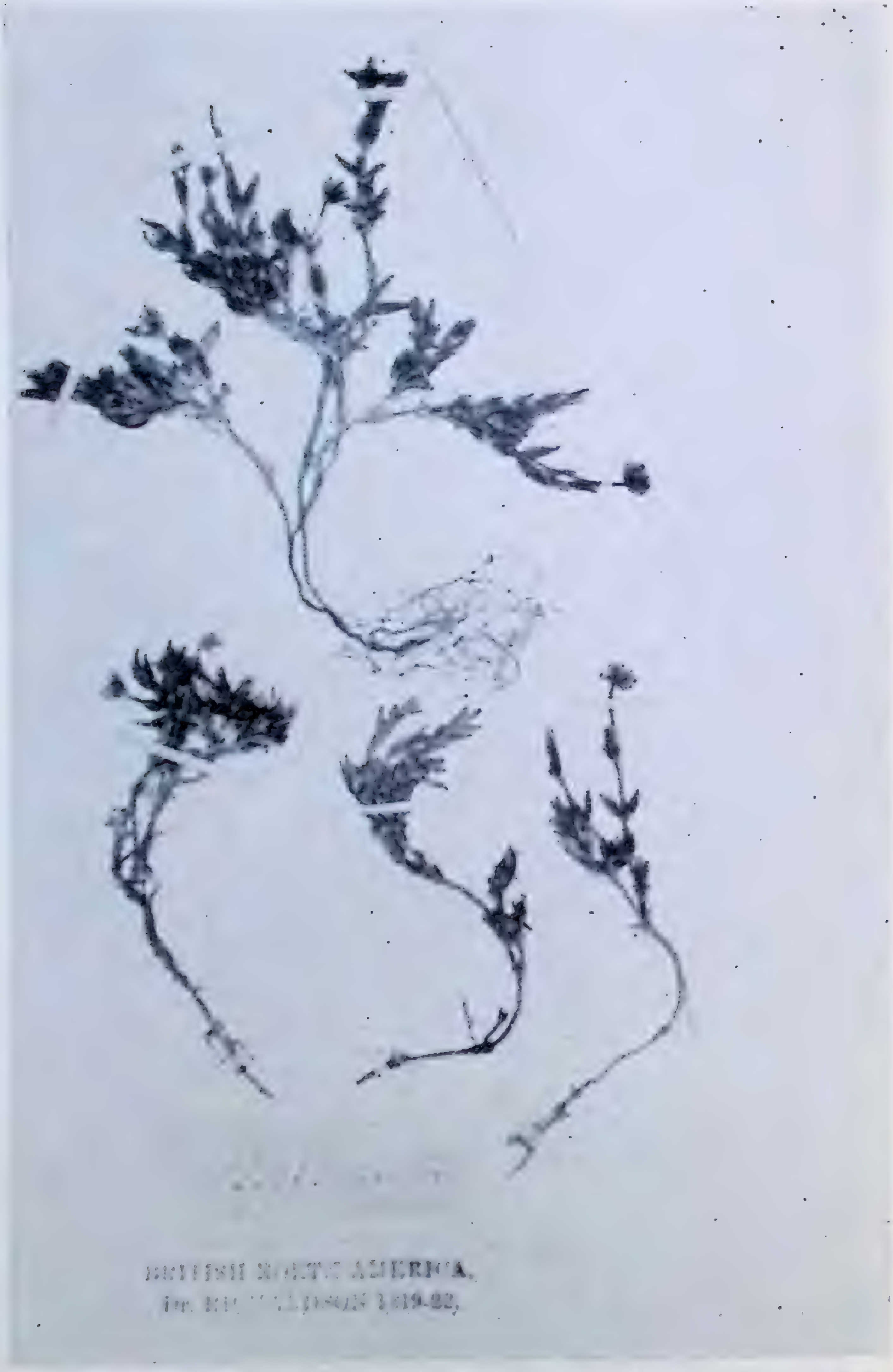


FIGURE 6. Total range of *Stellaria laeta* Richards.

PLATE VII



Lectotype of *Stellaria laeta* Richards. from "British North America," leg. Richardson. (BM). Approx. five-sixths nat. size

John Richardson, as is almost certainly that on the second label. Inasmuch as no type has been designated, I propose the specimens described above as lectotype for *Stellaria laeta* Richardson (Plate VII).

The distribution given for *S. laeta* in Fl. Bor.-Am. is "From Great Bear Lake to the shores and islands of the Arctic Sea," and as suggested by the maps published by Hultén, Böcher, and Porsild, its range is distinctly North American, barely reaching the tip of eastern Asia in the west, and in Greenland limited to the west and north coasts. Its general range is arctic or even high-arctic, reaching the northern tip of Ellesmere Island, but, as with *S. monantha* and *S. Edwardsii,* its southern limit is in the boreal forest. In the Canadian Rockies it follows a pattern set by a number of other mainly high-arctic species, thus far having been collected but a few times in widely disjunct places far above timberline where it is much less common than *S. monantha*. Hultén's map (l.c.) shows only one station, on Victoria Island, between Alaska-Yukon and the eastern Canadian Arctic. In my map (l.c.) its range is shown as complete from Northwest Greenland to Alaska, across the Arctic Archipelago, south to across the continent approximately to the treeline or slightly beyond, with isolated stations in the Rocky Mountains, south to lat. 51° 24′ N., in Alberta and British Columbia.

Among the arctic members of the *S. longipes* group, *S. laeta* appears to be the one that most regularly produces ripe fruits. Its capsules vary from almost black to pale brown or straw-coloured, averaging about 5 mm in length, or one-third longer than the sepals. The seeds are circular to short-oblong in outline and about 0.7 mm long. No chromosome count has been reported for this taxon.

Vegetative reproduction, by winter-green axillary buds, is common. The colour of the plants is commonly fresh green and shiny (although Richardson, l.c., described it as glaucous).

Little is known of the ecology of *S. laeta*. In my experience it is commonly found on mineral soil in damp sandy or gravelly places on flood-plains or on lake shores. In the arctic islands it often grows on moderately frost-heaved gravelly flats derived from weathered limestone or carbonate rocks. On the mainland, unlike *S. monantha,* it is rarely found in turfy places in tundra.

Map 6 shows the total range of *S. laeta*.

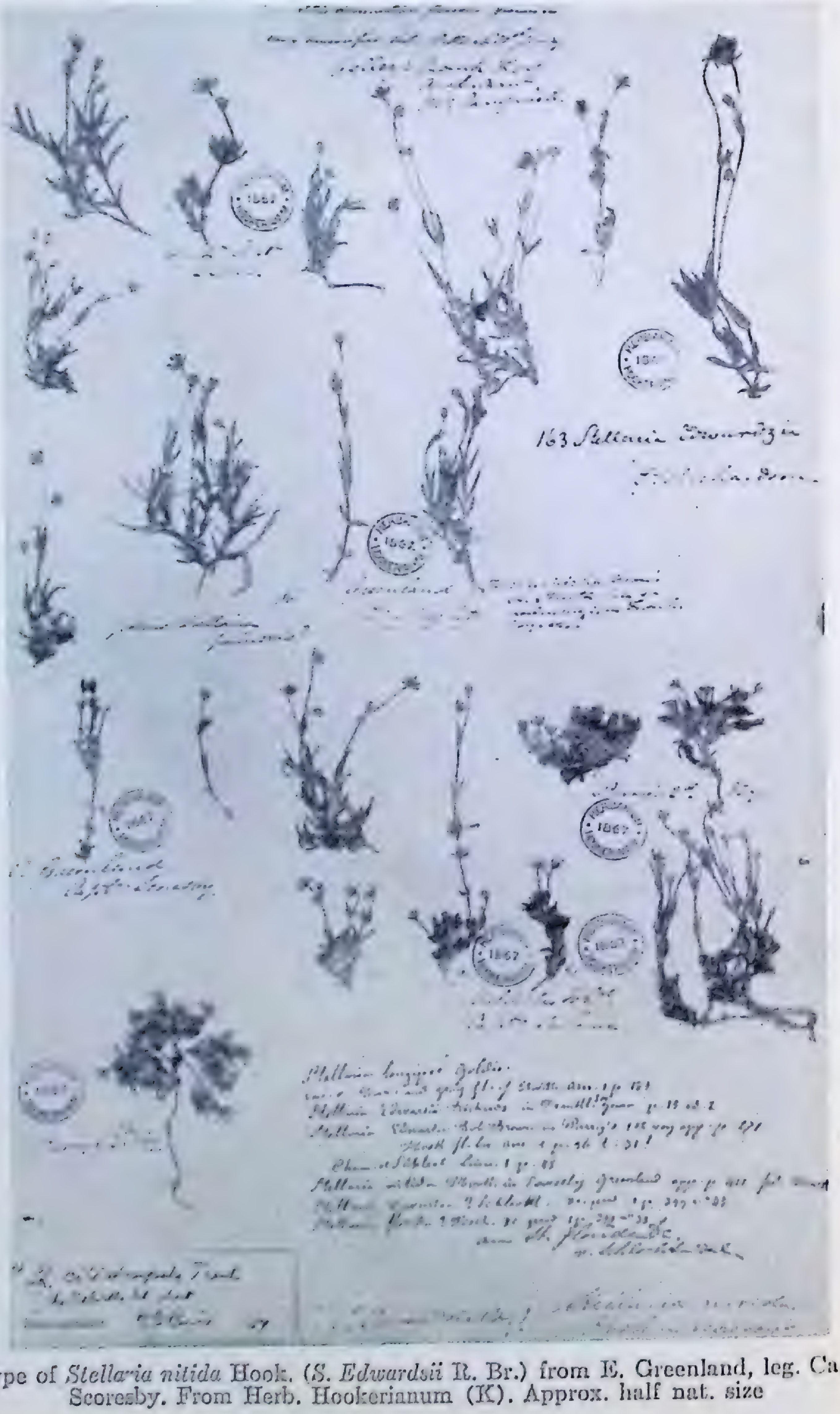
Stellaria Edwardsii R. Br. in Franklin, Narr. Journ. Polar Sea, App. vii, p. 738 (1823), Chloris Melvilliana, p. 13 (1823), and in "Supplement to the Appendix of Captain Parry's Voyage for the Discovery of a North-West Passage in the Years 1819–20," p. cclxxi (1824), London; Hooker, Fl. Bor.-Am., 1: 96 (1830), in part, and tab. 31.

S. nitida Hook., in Scoresby Voy. Northern Whale-Fishery, p. 411 (1823).

S. ciliatosepala Trautv. in Middendorff, Reise in d. äuss. Norden u. Osten Sibir. 2: 52 (1856), tab. 8, fig. 1; Hultén, Bot. Not. 1943, 257, fig. 5, a-c and map fig. 4; Böcher, Bot. Tidsskr. 48,4; 412 (1951) map fig. 5; Porsild, Nat. Mus. Canada, Bull. 135: 103–105 (1955); *idem, ibid.* 146: 75 (1957) fig. 29,c and map fig. 134.

S. ciliatosepala var. *arctica* (Schischkin) Hult., Hultén, l.c., 1943.

PLATE VIII



Type of *Stellaria nitida* Hook. (*S. Edwardsii* R. Br.) from E. Greenland, leg. Capt. Scoresby. From Herb. Hookerianum (K). Approx. half nat. size

The uncertainty as regards the true identity of *S. Edwardsii* R. Br. is, no doubt, in a large measure, due to Hooker's drawing (l.c.) and his failure to show the distinctive characters clearly described by Brown for his var. α ". . . bracteis semifoliaceis margine membranaceo ciliato," which omission undoubtedly caused Trautvetter (1856) to believe that his *S. ciliatosepala* from Taimyr in arctic Siberia was distinct from *S. Edwardsii* R. Br. The omission is the more surprising because Hooker clearly recognized his *S. nitida*[1] as being conspecific with *S. Edwardsii* and correctly placed it as a synonym of that species in Fl. Bor.-Am. Hooker, who in 1823 almost certainly had not seen the Parry collections, correctly noted that his plant differed from all other *Stellaria* then known or described by having "Pedicelli . . . ad basin bracteis duobus ovatis . . . membranaceis, marginibus diaphanis suffulti. Calyx . . . margine lato diaphano, albo, sub lente ciliato" and "Caules . . . basi subpurpurascentes atque pubescentes . . . ." *S. nitida* was described in a "List of plants from the East Coast of Greenland," presumably from specimens contributed mainly by Scoresby who, in his narrative, at least once mentions a search for plant specimens. In the case of *S. nitida*, Hooker, however, explicitly stated that the specimen "was communicated to me by the late Dr. Wright of Edinburgh, and gathered by his nephew, Dr. William Wright, in Greenland; but in what part of that interesting country, I have no means of ascertaining."

In the herbarium at Kew is a sheet from "Herbarium Hookerianum" that in the lower right corner is labelled in Hooker's handwriting, "*Stellaria nitida* Hook. in Scoresby's Voyage" (Plate VIII) and, to the left, in brackets, "*S. Edwardsii.*" On the sheet are mounted eight or possibly nine separate collections, most of them indubitably *S. Edwardsii;* among them three plants, mounted in the bottom centre of the sheet, are labelled "Melville Isl. Capt. Sabine." On the left side of the sheet, second from the bottom, are four plants labelled "E. Greenland. Capt. Scoresby," and in the second row from the top is written between the two plants in the centre "Greenland. Dr. Wright." I rather think that this was meant only for the plant to the left which is typical *S. Edwardsii*, because below and to the right of the second plant is written "This is Richardson's *St. stricta*: his *St. palustris β* in Frankl. Voy. ed. 1." It is strange, therefore, that in Fl. Bor.-Am., Hooker failed to mention the scarious bracts and the ciliate sepals that he had seen and described in his *S. nitida*, and which are clearly visible in the specimens shown on this sheet.

In the British Museum (Natural History) is a sheet of *Stellaria*, in the lower right corner labelled "Parry's First Voyage 1819–20, Melville Island." On the sheet are sixteen separate plants from three different collectors; each collection is labelled "*Stellaria Edwardsii*" and at the bottom of the sheet is stamped "Type Specimen" (Plate IX). The twelve plants mounted on the bottom half of the sheet are from the collection of James Ross[2] and show well-preserved flowering specimens. All have ciliate sepals and, when more than one flower is present, distinctly ciliate, scarious

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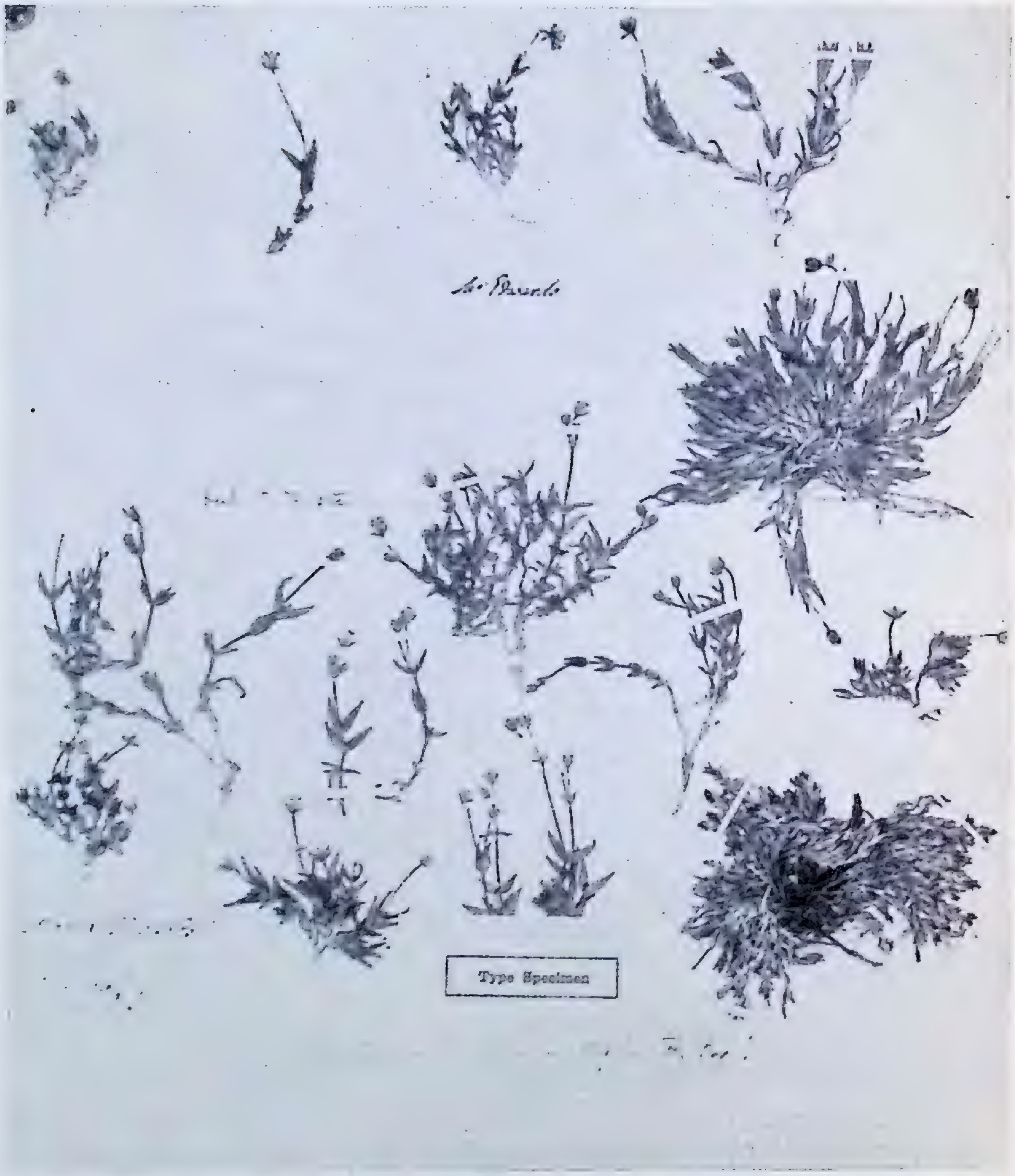
[1] Published after the appearance of "Chloris Melvilliana," but before the second and slightly amended reprinting, in 1824.

[2] Robert Brown (l.c.) stated that the plants enumerated in his "Chloris Melvilliana" are "from the Herbaria of Captain Sabine, Mr. Edwards, Mr. James Ross, Captain Parry, Mr. Fisher, and Mr. Beverly," all officers of Parry's First Voyage, 1819–20.

PLATE IX

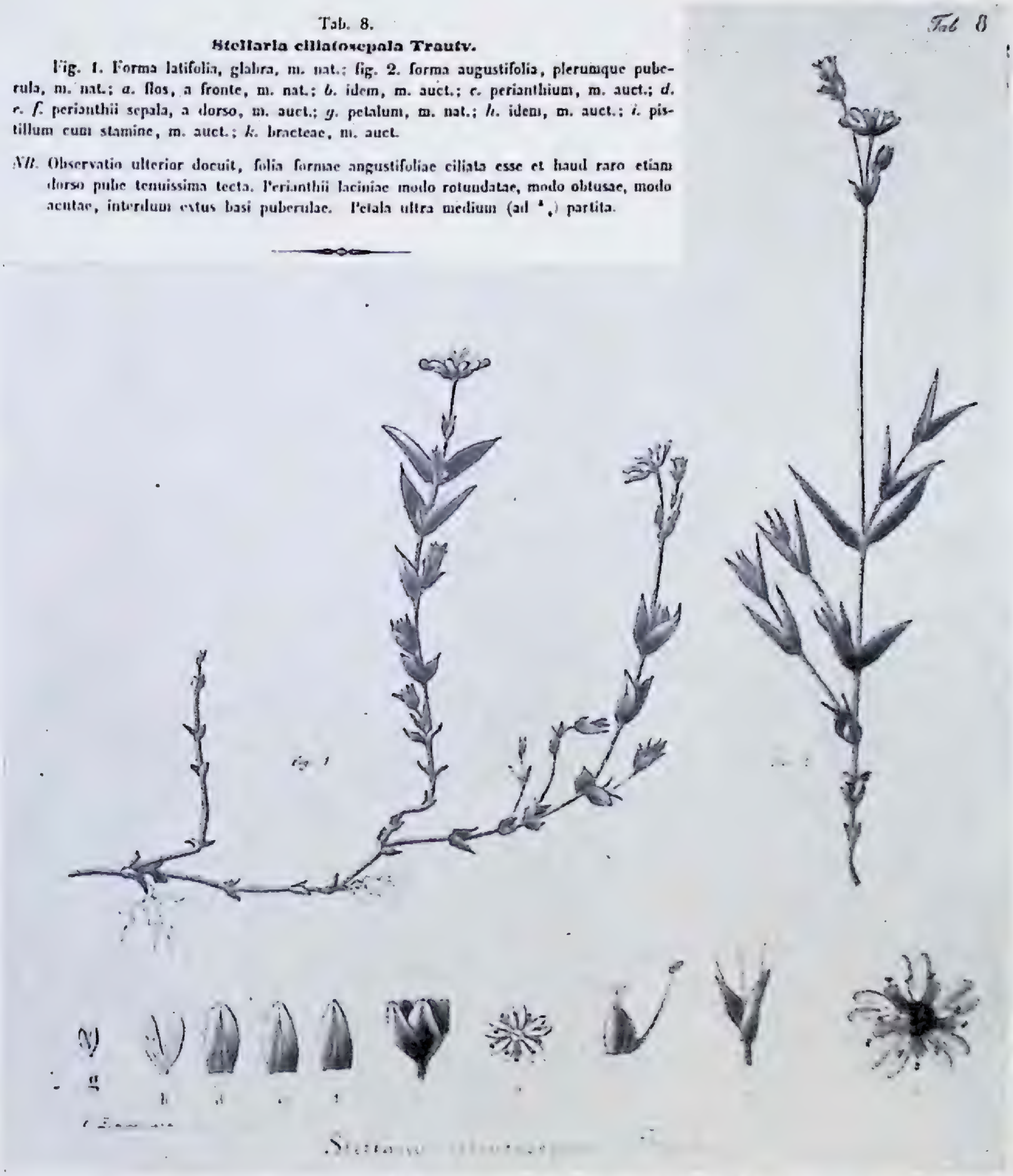


Type of *Stellaria Edwardsii* R. Br., from Melville Island, N.W.T., Canada, from Parry's First Voyage, 1819–20 (BM). Approx. half nat. size

bracts. These obviously are the plants which Brown designated var. *α*. They also agree in every respect with Trautvetter's (l.c.) excellent description and fine drawing of his *S. ciliatosepala* (Plate X).

On the upper left corner of the Parry sheet in the British Museum (Plate IX) are two rather scrappy plants collected by Sabine, and on the upper right corner are two somewhat better specimens from the collection of Edwards. These all have single flowers and ciliate-pubescent sepals

PLATE X



Tab. 8.

Stellaria ciliatosepala Trautv.

Fig. 1. Forma latifolia, glabra, m. nat.; fig. 2. forma augustifolia, plerumque puberula, m. nat.; *a.* flos, a fronte, m. nat.; *b.* idem, m. auct.; *c.* perianthium, m. auct.; *d. e. f.* perianthii sepala, a dorso, m. auct.; *g.* petalum, m. nat.; *h.* idem, m. auct.; *i.* pistillum cum stamine, m. auct.; *k.* bracteae, m. auct.

NB. Observatio ulterior docuit, folia formae angustifoliae ciliata esse et haud raro etiam dorso pube tenuissima tecta. Perianthii laciniae modo rotundatae, modo obtusae, modo acutae, interdum extus basi puberulae. Petala ultra medium (ad [illegible]) partita.

Stellaria ciliatosepala Trautv. in Middendorff, Reise in d. äuss. Norden u. Osten Sibir., tab. 8

but lack scarious bracts and, therefore, agree with *S. laeta* Richards. They are obviously the plants which Hooker assigned to *S. Edwardsii* var. *β*. An examination of the numerous sheets of *Stellaria* from the Canadian Arctic in the Hooker Herbarium at Kew failed to identify equivocally the original plants from which Hooker drew his Tab. xxxi. Those most likely to have served are on a sheet of miscellaneous collections labelled

"*Stellaria longipes* Goldie," on which two plants, mounted on the bottom part of the sheet, are marked "Arctic Islands. Parry." Both are *S. Edwardsii*, but only the plant on the left shows a pair of poorly developed scarious bracts.

Stellaria Edwardsii is circumpolar and of distinctly arctic range, although in central Alaska and Yukon it extends far south of the treeline. To the maps published by Hultén (l.c.) and Böcher (l.c.) should be added the numerous North American stations shown by me (l.c., map 134), most of them listed (Porsild, 1955, p. 104). Although in *S. Edwardsii* the incidence of pubescent internodes appears to be higher in Alaska and Yukon than in the central Canadian Arctic, it seems doubtful if any geographic significance can be attached to this, because in the somewhat disjunct population of *S. Edwardsii* on the coast of Labrador the internodes appear to be equally pubescent. A similar condition apparently exists in Siberia. Trautvetter's Tab. 8 shows one plant (left) with glabrous stem and leaves, and another (right) in which the lower internodes, branches, and leaves are shown to be pubescent (Plate X).

Alerted by Böcher's report (l.c., 412) of a single, disjunct station of *C. ciliatosepala* [*S. Edwardsii*] from Cartwright on the southern Labrador coast, I re-examined material in the National Herbarium, by me previously referred to *S. longipes* s. str. This brought to light additional collections that clearly are more closely related to *S. Edwardsii* than to typical *S. longipes* s. str. All have pubescent internodes, and on nearly all sepals a few ciliae are visible under a low-powered microscope. To my list, cited above, should thus be added: Okak, lat. 57° 40′ N., Wynne-Edwards 7511; Turnavik, lat. 56°16′ N., Porsild 104; Cutthroat Hb., south of Cape Mugford, lat. 57°30′ N., Porsild 184; Cartwright, lat. 53°42′ N., Malte CAN 119851; Gready Island, lat. 53°48′ N., Forbes 290, and Gready Hb., Soper CAN 111657.

In the interior of Alaska and Yukon *S. Edwardsii* is often very high-grown, with stems up to 30 cm high, and with large flowers in which the petals may be 8 mm long: Chandler R., lat. 69° 26′ N., elev. 140 ft., Chambers 149.

Jørgensen, Sørensen, and Westergaard (1958) reported that chromosome counts on root-tips in plants from Clavering Island in Northeast Greenland of 2=91 and, because the basic number in this group is 13, assumed this taxon to be of hybrid origin. They state further that "sexual reproduction is very scarce, if any, since only female plants seem to exist." In my experience, perfect flowers appear to be the rule. An examination of ninety-one collections of *S. Edwardsii* [*S. ciliatosepala* Trautv.] in the National Herbarium of Canada, representing specimens from Northeast Greenland to Alaska, brought to light only two sheets on which all flowers are pistillate. Among the seventy-six collections with normal, bisexual flowers, thirty-two appear to have normal pollen, in twenty-five the pollen sacs are not yet open, and nineteen have fruits in various stages of development, including several in which the seeds appear fully ripe. Most of the remaining thirteen collections were either too fragmentary or showed only last years' frost-damaged flowers. The examination clearly shows that flowering and fruiting appear to be normal in this taxon. Furthermore, Trautvetter's illustration (l.c.) of *S. ciliatosepala* shows normal, bisexual flowers, as does Hooker's (l.c.) drawing of *S. Edwardsii.*

The North American range of *S. Edwardsii* is shown on map fig. 7.

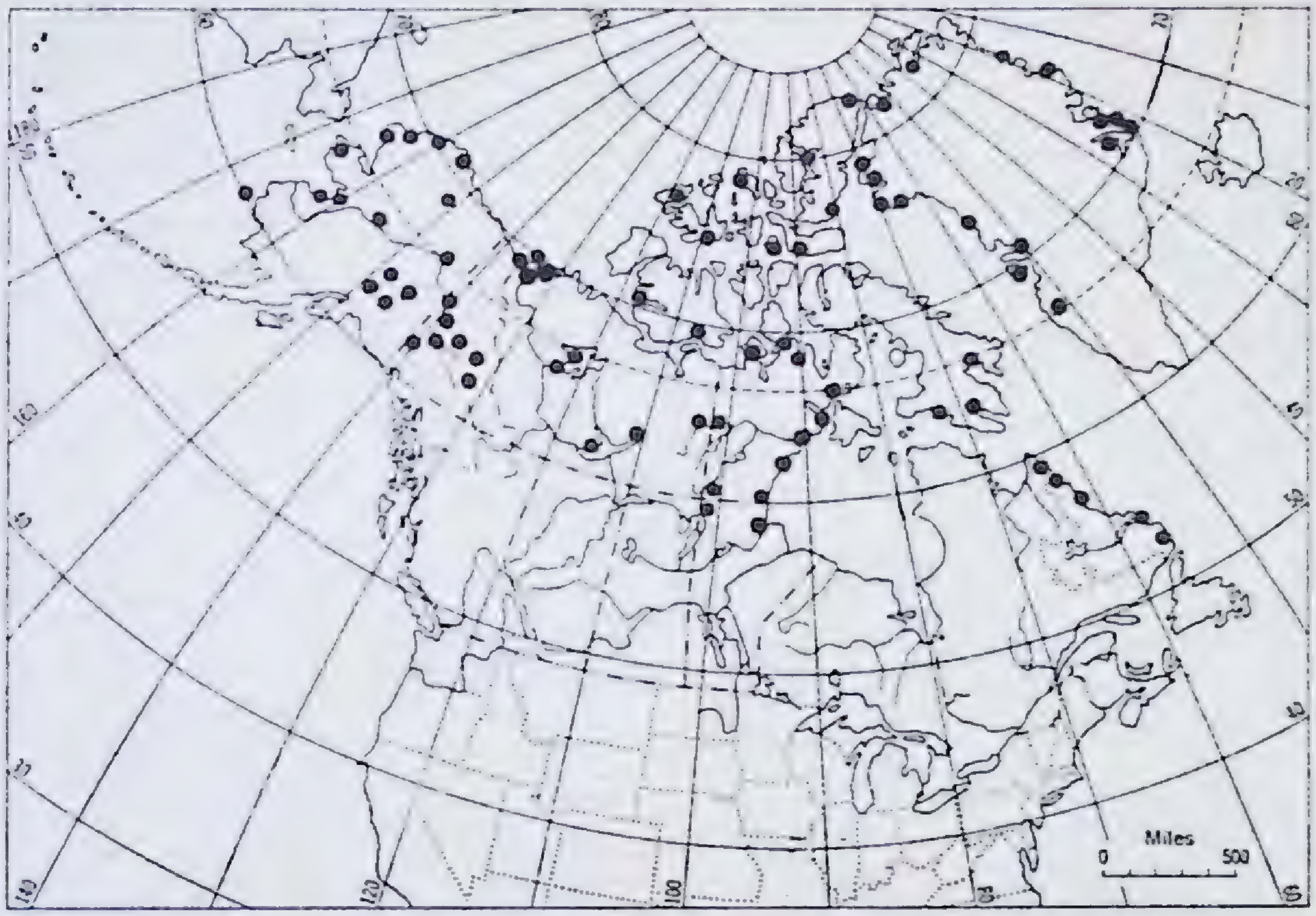


FIGURE 7. North American range of *Stellaria Edwardsii* R. Br.

Stellaria sp.

S. Laxmanni sensu Hultén in Bot. Not. 1943, p. 261 and fig. 5 d, and Fl. Alaska & Yukon, 4: 655 (1944) and 10: 1738 (1950), not Fisch. ex Ser. in DC., Prodr., 1: 397 (1824), nor Ledeb. Fl. Alt., 2: 158 (1830), nor Ledeb. Ic. Pl. Fl. Ross. tab. 423 (1834).

Hultén (l.c.) reported *S. "Laxmanni"* from six stations in Alaska and Yukon; the writer (Porsild, 1951) added three more from Southeast Yukon. A few more recent collections are in the National Herbarium of Canada: Yukon: Alaska Highway between Chicago Creek and Whitehorse, Porsild 22343; Alaska: White Mountains, Gjaerevoll 771; Gerstle R., Spetzman 590; Umiat, Bormann 70BC.

According to Hultén, this plant has "sepals densely pubescent on the back, especially towards the tip," and by this character alone, combined with its commonly many-flowered inflorescence in which the peduncles are supported by scarious bracts, it differs from all other members of the *S. longipes* complex. One other character, not mentioned by Hultén, although at least two of the specimens cited by him possess it, is a dense but short pubescence on the internodes, present for example in specimens from Whitehorse (Anderson 9657) and "from back of Dawson" (Macoun, CAN 58414, in part). In some other specimens before me, the internodes are perfectly glabrous, and in others from Yukon the leaves bear long, soft hair on both surfaces (Canol Road, Lapie Crossing, Porsild 9832), though in some others the leaves are only ciliate in the margins. Anderson's No. 9657 has fully developed capsules one-third longer than the sepals, but most of them are empty or contain a few but apparently normal seeds that are almost spherical and strongly pebbled, whereas in Spetzman's No. 590 all capsules contain seeds that are distinctly oblong. Finally, Bormann's No. 70B, from Umiat, bears a strong resemblance to *S. Edwardsii*, except that the sepals are densely short-pubescent.

In Yukon and Alaska, but only within the range of Hultén's *S. "Laxmanni,"* two other "races" occur that, because they commonly have pubescent sepals and lack scarious bracts, could be referred to *S. laeta*, although they do not have the habit of that taxon. One of these "races," apparently restricted to alpine situations, has the habit of *S. Edwardsii* and has thinly pubescent internodes: S.W. Yukon: Kluane Lake, mountains above Vulcan Creek, Schofield & Crum 8203. This is a peculiar looking plant with fresh green, spreading leaves and a single terminal and long-peduncled flower. Alaska: Alaska Range, near Black Rapids Glacier, Gjaerevoll 1481; White Mountains, headwaters of Sheep and Mascot creeks, Gjaerevoll 189; Wiseman, Anderson 5886. The second "race," from sandy lowland stations, commonly on disturbed soil near or along road embankments, has the habit of *S. subvestita*, with short, densely villose internodes and leaves that are sometimes glabrous and shining but more commonly villose dorsally, on the midrib and on the margins—Yukon: Miles Canyon near Whitehorse, M. P. and R. T. Porsild 67; Takhini R. between Whitehorse and Champagne, Michel 11; Makintosh, Alaska Highway, Mile 1022–1037, Schofield & Crum 7623 and 7732. Alaska: Nabesna Rd., roadsides, Dutilly, Lepage, and O'Neill 21520; on old sandy road, Slana, Dutilly, *et al.*, 21642; Glen Rd., roadsides, Mile 124, Dutilly, *et al.* 20413; near head of Chitina River, Laing 50.

Several, if not all, members of the *S. longipes* complex are of notoriously weedy habit and are known as pioneers on disturbed soil. On the west coast of Greenland, M. P. Porsild (1932) noted that *S. longipes* (s. lat.) is among the first plants to colonize recently denuded soil and, in gardens, becomes a "pertinacious and troublesome weed." Under less arctic conditions, when at least some members of this group reproduce freely by seed, as well as by vegetative means, their ability to spread and to colonize freshly disturbed soil, naturally is even greater, as are facilities for spreading, in which they are no doubt greatly aided by modern road-building techniques, and by road-building and road-maintenance machinery that in the course of construction is moved rapidly by trailers from one construction site to another and often from great distances. The caterpillar treads of these machines, as well as the scoops of power shovels and earth-moving equipment, inevitably must carry soil, and with it seeds of plants, from one construction site to another. Also, the treads of automobiles and trucks, especially those employed on construction jobs, readily pick up soil and the seeds of weedy species growing by the roadside.[1]

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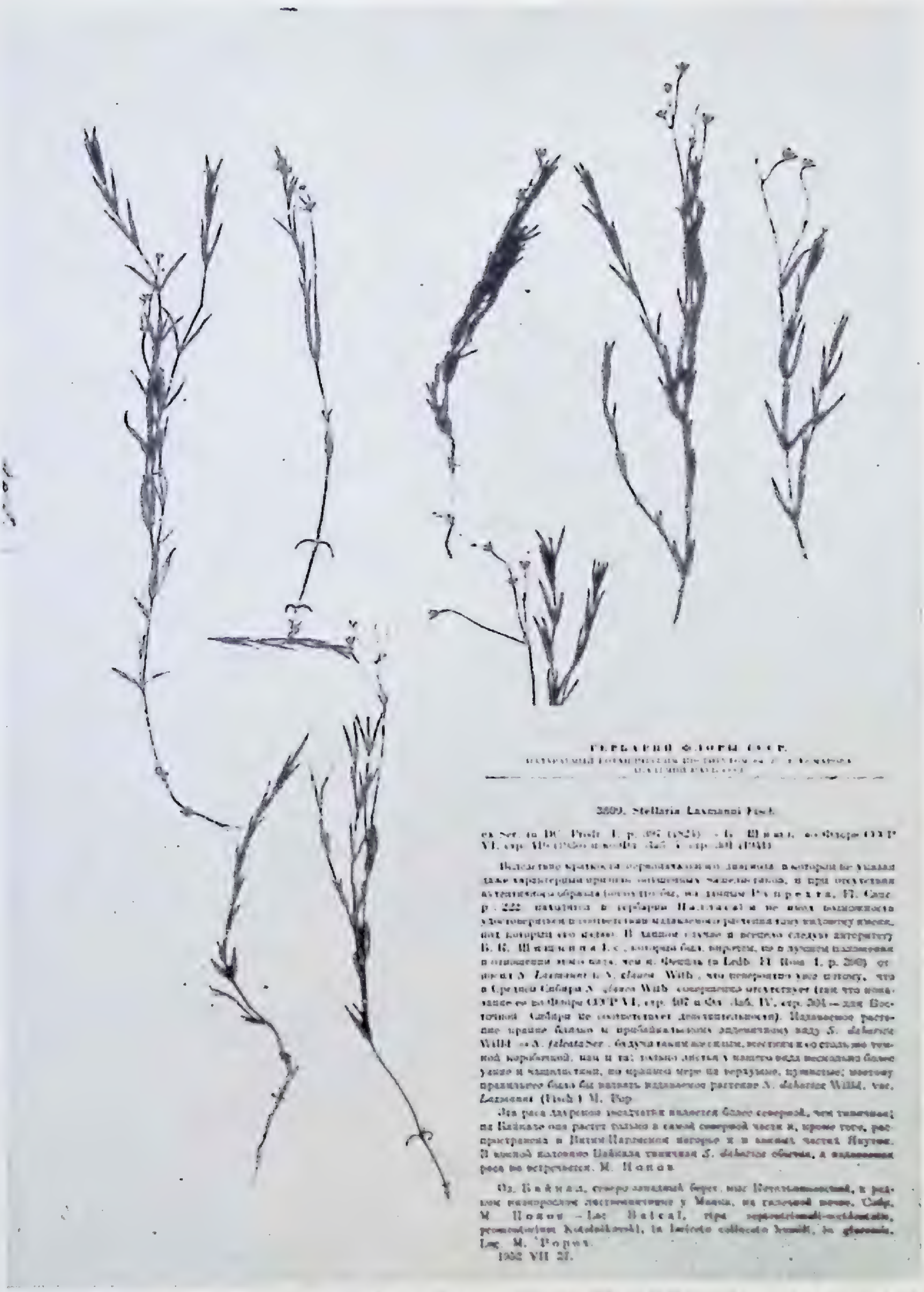
[1] In the construction of the military road, now known as the Alaska Highway, and of the now abandoned Canol Road, a number of construction companies participated, all operating and hauling road equipment from centres in the western and central United States or from Alberta and British Columbia.

PLATE XI



Stellaria Laxmanni Fisch., No. 3809 of Exsicc. Herb. Fl. S.S.S.R., from Lake Baical, Siberia. leg. M. Popov (CAN 246982)

In the interior of Yukon and Alaska, several members of the *S. longipes* group, as well as a great many other native or introduced weedy species, have taken full advantage of this man-made opportunity or "free travel" (*see also* Porsild, 1951, pp. 34–35, and 1961, pp. 174 and 181). In interior Yukon, the western *S. subvestita* and *S. stricta* are common along highways and on other man-made sites, and from personal observations in the field and examination of herbarium specimens it would appear that *S. longipes* s. str. in Yukon and Alaska occurs only in such places and, in other words, that it is not indigenous to the flora.

Only in the interior of Yukon and Alaska do the ranges of members of the *Stellaria longipes* group, having ciliate or pubescent sepals (*S. Edwardsii* and *S. laeta*), extend far into the boreal forest region, and only in that part of North America are there now man-made meeting grounds providing opportunities for hybridization between these and the high-grown and more southern taxa with glabrous sepals and scarious bracts in the inflorescence. *Stellaria "Laxmanni"* sensu Hultén, which has scarious bracts, pubescent sepals, and pubescent or even villose internodes and leaves, or a combination of these characters, surely could well be the result of such crossings. At any rate, it is not the Siberian *S. Laxmanni.*

The original description of *Stellaria Laxmanni* Fisch., ex Ser. (l.c.) is so general that it fits almost any member of the *S. longipes* group. No reference is made to its sepals. In Fl. Alt., on the other hand (l.c.), *S. Laxmanni* is explicitly stated to have glabrous and non-ciliate sepals. In Ledeb. Fl. Rossica, 1: 390 (1842) it was reduced to synonymy under *S. glauca* var. β *virens.*

From the discussion given by Schischkin (Fl. S.S.S.R., vi: 416–7) it appears that the identity of *S. Laxmanni* Fisch. is still not clear. An examination of specimens in the Leningrad Herbarium in 1957 fully confirmed this, convincing me as well of the absence there of Asiatic specimens similar to the Alaska-Yukon plant to which Hultén (1942), somewhat tentatively, applied that binomial.

Stellaria Laxmanni Fisch., No. 3809 of Exsicc. Herbarium Flora S.S.S.R., from "*Lac. Baical, ripa septentrionali-occidentalis, promontorium Kotelnikovski, in lariceto collugato humili, in glareosis.* Leg. M. Popov, 1952 vii 27" clearly represents the taxon illustrated by Ledeb. Ic. Pl. Fl. Ross. tab. 423. In general habit Herb. Fl. S.S.S.R., No. 3809 resembles a few-flowered *S. stricta* Richards. and, like it, is glabrous, but of the seven plants on a duplicate sheet of that number in Ottawa (CAN 246982) (Plate XI), each with from 3- to 5-flowered cymes, one has flowers in which the sepals are prominently pubescent on the back, in two plants the sepals are only ciliate-margined, and in the rest the sepals are perfectly glabrous. On still another duplicate sheet, at Kew, the sepals in most of the flowers are pubescent on the back.

CONCLUSION

The present revision of the North American members of the *Stellaria longipes* group is based on considerable field experience with all members of the group, except *S. arenicola* Raup, and on the study of more than 800 herbarium specimens, assembled mainly in the National Herbarium of

Canada, together with the study of all known types or type material, in the herbaria of Kew Botanic Gardens and the British Museum (Natural History), London, and in the Botanical Institute of the U.S.S.R. Academy of Sciences, Leningrad, as well as of the original descriptions of all pertinent taxa.

On the basis of this study, the writer recognizes eight taxa of more or less well-defined geographical ranges as native to North America. Of these only *S. Edwardsii* R.Br. is of truly circumpolar, arctic range; *S. crassipes* Hult., formerly known to be of amphi-Atlantic range, may prove to be circumpolar, although as yet with large gaps. The remaining six are North American. Among the latter, *S. longipes* Goldie s. str. and *S. arenicola* Raup are boreal forest species, the last thus far known only from the type locality. *S. subvestita* Greene and *S. stricta* Richards. are western prairie and foothill species with ranges barely extending north beyond the treeline. *S. laeta* Richards. and *S. monantha* Hult. are wide-ranging and essentially arctic species, the first with a North American range very similar to that of *S. Edwardsii* R. Br. but in common with *S. laeta* is absent in East Greenland; on the N. American mainland the ranges of all three extended south into the northern fringe of the boreal forest.

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ENCALYPTA BREVICOLLA AND *E. LONGICOLLA* IN NORTH AMERICA

By Howard Crum

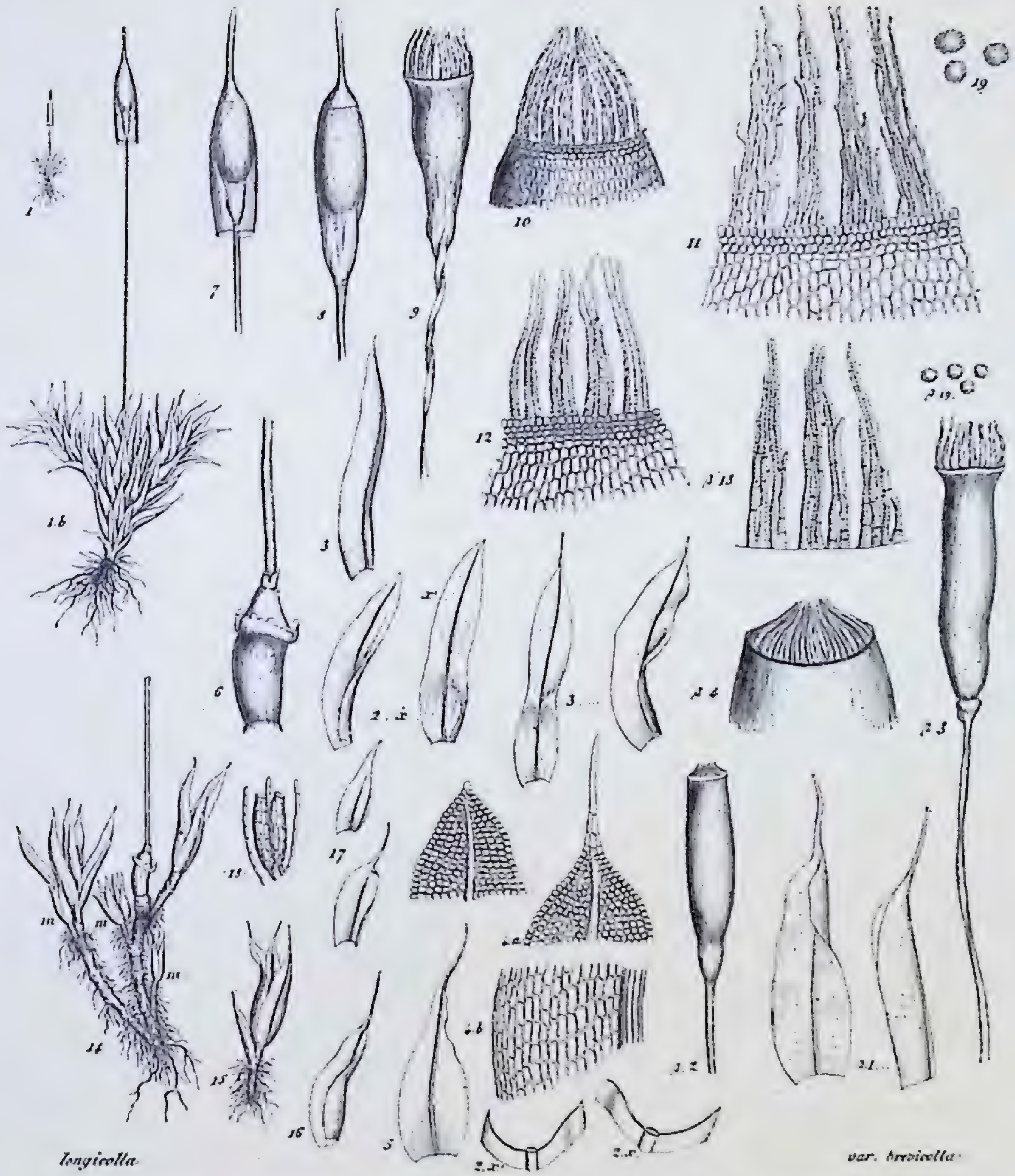
In his revision of the genus *Encalypta* in North America, Flowers (1938) was forced to draw his description of *E. brevicolla* (BSG) Bruch ex C.M. from European specimens and from other authors because no American specimens were available for study. He noted that the species had been reported from Labrador and the east coast of Greenland. Coker (1918) had given the distribution as "Labrador and, according to the Paris Index, the eastern coast of Greenland."

The record from Labrador was based on the types of *E. labradorica* Kindb. (from Fort Chimo) and *E. subbrevicolla* Kindb. (from Seal Lake), which Miss Coker correctly assigned to the synonymy of *E. brevicolla*. Both specimens, collected by A. P. Low in 1896, came from the part of "Labrador" now politically assigned to the province of Quebec.

The record from eastern Greenland seems to have been based on *Leersia laciniata* var. *groenlandica* C. Jens., collected on Danmarks Ø, Scoresby Sund, by N. Hartz in 1891–92. I have not seen the name listed in any published synonymy, but Scoresby Sund is cited under *E. brevicolla* in Paris's *Index Muscorum* (ed. 2, vol. 2, p. 120. 1904). I have seen two reprints of Jensen's article in which the "var. *groenlandica*" is altered in Morten Porsild's hand to read "*brevicolla* (Bruch) Lindb. i følge C. J." (According to a letter from Kjeld Holmen, Jensen realized the synonymy before reprints were distributed and altered them himself.) Unfortunately, no type was designated, and no specimens in Jensen's herbarium at Copenhagen bear the varietal name, but three specimens collected by Hartz on Danmarks Ø are labelled *E. brevicolla*, apparently by Jensen. Since *E. brevicolla* was not included in the published report of Hartz's moss collections, the variety must have been based on these specimens. One of them is *E. alpina* Sm. (sterile), a second is a mixture of *E. alpina* (sterile) and *E. brevicolla* (*c.fr.*), and the last is *E. brevicolla* (*c.fr.*).

Brotherus (1923) cited numerous localities in Finland, Norway, and Sweden and mentioned the occurrence of the species in North America; he described the habitat as "auf trockenen, humusbedeckten Felsabhängen und in erdfüllten Felsspalten, besonders von Schiefer und Granit." The following year (1924), he summarized the distribution as "Fennoskandia, Sibir., in erdigen Felsspalten kalkarmer Felsarten." Other, more recent authors have indicated a preference for calcium: Mårtensson (1956) reported that in northern Swedish Lappland the species "prefers warm, protected habitats, where it grows on soil-covered rocks (limestone, dolomite a.o) or crevices in cliffs etc.," in the subalpine and lower parts of the low-alpine belts. Nyholm (1956) reported the Fennoscandian habitats as "dry soil or in rock crevices, preferably in calcareous districts, from the lowlands to the mountains." Persson and Gjaerevoll (1957) said of an Alaskan collection, "In Scandinavia this is a species of calcareous soils. The mountains at the headwaters of Sourdough Creek [Alaska] are built up by

PLATE I



Encalypta longicolla and *E. brevicolla.* Figs. 1–11, 14–19. *E. longicolla.* *1.* Plants. *2.* Lower leaves. *3.* Upper leaves. *4.* Leaf cells. *5.* Perichaetial leaves. *6.* Vaginula (filiform paraphyses and archegonia not shown). *7.* Calyptra (fringed base not shown). *8, 9.* Gross sporophytic features. *10, 11.* Peristome. *14, 15.* Perigonia. *16, 17.* Perigonial bracts. *18.* Antheridia with paraphyses. *19.* Spores. Figs. 12 and β 1, 3, 4, 13, and 19. *Encalypta brevicolla.* β1. Leaves. β3. Sporophyte. β4, 12, and β13. Peristome. β19. Spores.

—From the *Bryologia Europæa,* vol. 3, plate 202

'Birch Creek schists' (pre-Cambrian) and are rich in calciphilous species." Persson (1952) stated that *E. brevicolla* is subalpine and continental in its Fennoscandian distribution.

The only Siberian collections, apparently, were made in 1898 by H. Nilsson-Ehle in the Lena River Valley, at "Kumachsur, fr., mehrfach gesammelt, so z.B. an Felsen oder unter Steinen an einem Süd-Abhang; hiervon stammt auch eine *forma gymnostoma*" (Arnell, 1913).

Collections of *E. brevicolla* have been reported from several North American localities besides those referred to by Coker or Flowers. Williams (1921) reported it from Barter Island, off the arctic coast of Alaska. The specimens at the National Museum of Canada and the New York Botanical Garden, collected during the Canadian Arctic Expedition in 1918 by J. Hadley, consist of a few sterile plants in poor condition. The leaves are scarcely contorted, as typical of *E. brevicolla*, and in this way, as well as in shape, they are strongly suggestive of *E. alpina* Sm. instead. I consider the specimen indeterminable; in any case, it is not *E. brevicolla*.

Harvill (1950) reported a specimen from Fairbanks, Alaska (*T. L. Péwé* M73b). According to Harvill's paper, the specimen should be at the herbarium of the University of Michigan; I recently examined all the mounted material of *Encalypta* at the University of Michigan but failed to find such a specimen. (Dr. Harvill has written me to say that he did not retain a specimen for his own herbarium.)

Persson (1952) cited a collection from Umiat, just north of the Brooks Range in northern Alaska (*E. Lepage* 22,566), and Persson and Gjaerevoll (1957) contributed another Alaskan record, from the headwaters of Sourdough Creek (about 160 miles northeast of Fairbanks on the Steese Highway to Circle City). I have confirmed these records.

Over a period of several years I have accumulated records and confirmed previous reports of *E. brevicolla*, which is unquestionably rare but quite widespread in the Western Hemisphere. I have seen a total of 42 specimens from the New World (from Greenland, Baffin Island, the northern tip of Quebec, Great Bear Lake, Alberta, British Columbia, and Alaska). I have also seen numerous collections from Norway and Sweden. Of all the North American specimens cited in full below, only those collected by Low in "Labrador" and Lepage and Gjaerevoll in Alaska have been reported in the literature before. All the others, therefore, represent first records and range extensions of considerable interest.

Unfortunately, many of the American specimens are lacking in habitat data, and the available information is too vague to permit ecological generalization. However, it appears that *E. brevicolla* grows in the usual habitats occupied by the genus, on thin soil or humus in sheltered crevices of rocks and cliffs or in depressions of banks. No preference for calcium can be demonstrated, but it can probably be assumed that the species has much the same ecological predilections in the New World as in the Old and probably prefers but does not demand a limey substratum.

As mentioned above, Persson and Gjaerevoll reported the species from an Alaskan area rich in calcicoles. Dr. Charles D. Bird, who collected *E. brevicolla* in Jasper National Park, where the rocks are calcareous and the flora decidedly calciphilous, sent (in a letter) some additional information on associated species, some of which indicate a presence of calcium:

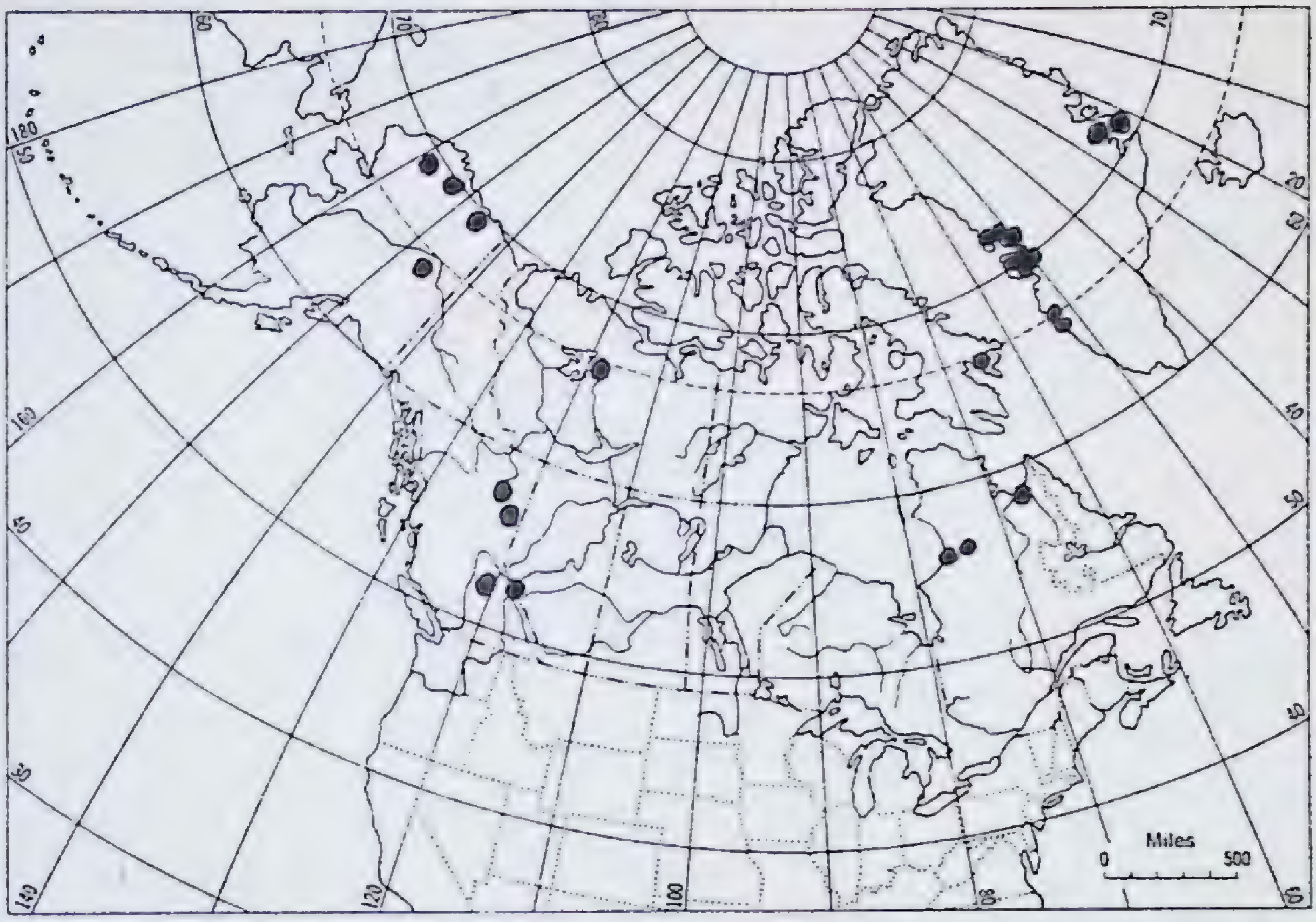


FIGURE 1. The distribution of *Encalypta brevicolla* in the Western Hemisphere

It was growing with *Cnestrum schisti* on a scree boulder. "Other mosses collected in the same area were *Bartramia ithyphylla, Encalypta rhabdocarpa* var. *subspathulata, Grimmia affinis, G. apocarpa* var. *conferta* fo. *obtusifolia, Orthotrichum macounii,* and *O. alpestre.*" One Greenland collection came from an obviously calcareous substratum—bones in old Eskimo tombs! Only seven labels gave any indication of the type of rock-gneiss (4), diabase trap rock (2), and granitic rock (1). Of the remainder, seventeen came from the surface or crevices of rocks and cliffs of unspecified nature, one from soil among boulders, one from a stream bank, and one from a dry *Betula nana* heath.

Encalypta brevicolla is very easy to recognize because of its very pale, faintly yellowish or off-white peristome which becomes bone-white with age. Other helpful characters include the hyaline-awned leaves which are keeled and contorted when dry, the capsules which are smooth (or finally becoming very faintly shrivelled in longitudinal lines), the narrowly lanceolate teeth of the exostome to which the endostome segments adhere, and the large, moderately warty spores, measuring 29 to 40 μ in longer diameter. The species has been confused, through carelessness no doubt, with *E. ciliata* Hedw., which is immediately separable because of its single peristome of red-brown teeth and its very distinctive spores with an irregular pattern of wrinkles. *Encalypta affinis* Hedw. f. ex Web. & Mohr has a peristome similarly doubled, but the teeth are reddish and more slender, and the spores are smaller and finely papillose. Some specimens of *E. vul-*

garis Hedw. have a pale, fragmentary peristome suggestive of that of *E brevicolla*, but it is single and less regular in outline. Since the spores are similar in size and sculpturing in the two species, confusion may result. (*E. vulgaris* ordinarily has clearly ribbed capsules. However, a specimen from British Columbia, issued as Grout's *North American Musci Perfecti* 108, has only lightly ribbed capsules with a whitish peristome of fair development so that it bears an unfortunate, though superficial resemblance to *E. brevicolla*.)

The diagnostic features are illustrated by plate 202 published in the *Bryologia Europæa*, reproduced here as Plate I.

SPECIMENS EXAMINED[1]

GREENLAND: North coast of Kangiussaq at sharp inner bend of Evighedsfjord, 65°53′ N., 52°15′ W., *T. Christensen*, July 4, 1958 (C); on moist crevices of gneissic and granitic rocks, 100–150 m. alt., S.W. coast of Rypefjord, 71°02′ N., 27°45′ W., *K. Holmen* 18955, 19025, July 30, 1958 (C); Danmarks Ø, *N. Hartz*, June 1892 (C): Havnen, Scoresby Sund, *O. Hagerup*, Aug. 24, 1924 (C); S. O. Bugten v. Christianshaab, *J. Vahl* (C); Naqsutokfjord (=Nordre Stromfjord), 67°28′ N., *Kornerup*, July 22, 1879 (C); in locis humidis ad pedes alpinum sinus Isortok, *J. Vahl*, 1832 (C); Itsako, Svartenhuk Peninsula, 71°39′ N., 53°50′ W., *K. Holmen* 10362, Aug. 23, 1950 (C); S.-exposed scree, Sagdliaruseq, Inukavsait Fjord, Qoiqe Peninsula, 71°19′ N., 52°16′ W., *K. Holmen* 16830, July 25, 1956 (C; CAN); in rock crevice, Inukavsait Fjord, Qoiqe Peninsula, 71°15′ N., 52°16′ W., *K. Holmen* 16260, July 23, 1956 (C); Esersiutilik, head of Kangerdluarssuk Fjord, 71°17′ N., 51°32′ W., *K. Holmen* 13816, July 28, 1956 (C); moist rock crevices, same loc., *K. Holmen* 16793, July 27, 1956 (C; CAN); in dry *Betula nana* heath, Kangerdluarssuk, Disko Fjord, 69°30′ N., 53°33′ W., *K. Holmen* 14145, June 20, 1956 (C); Eqalungiut Itivnerit, Disko Fjord, *M. P. Porsild* 2911, Sept. 6, 1898 (C); on gneissic rock shelves, Godhavn, 69°15′ N., 53°33′ W., *K. Holmen* 14199, June 11, 1956 (C); on moist crevice of gneissic rock, same loc., *K. Holmen* 14361, June 8, 1956 (C); on bones in old Eskimo tombs, Jakobshavn, 69°13′ N., 51°06′ W., *K. Holmen* 16037, Sept. 8, 1956 (C); on dry rock, Uvkusigssat, 71°03′N., 51°53′ W., *K. Holmen* 15832, July 16, 1956 (C); in locis humidis. . .Sakkane distr., Colon Rittenbenk, *J. Vahl*, Aug. 1835 (C).

ALASKA: Near a brook, headwaters of Sourdough Creek, White Mts., Central Yukon District, *O. Gjaerevoll* 1030, Aug. 8, 1953 (TRH). On soil, crevices between boulders, ca. 3,000 ft. alt., southwest end of Chandler Lake, Endicott Mountains, Brooks Range, ca. 68° 12′ N., 152° 47′ W., *W. C. Steere* 18514, July 19–24, 1952 (CAN); on rocks, Umiat, *E. Lepage* 22566b, d. July 30, 1948 (S-PA); in rock crevices, 1,000–1,100 m alt., Lake Peters–Lake Schader, Brooks Range, 69°20′ N., 145° W., *W. C. Steere, O. Mårtensson*, and *K. Holmen* 60–964, 60–1207, July 23, 27, 1960 (C); at 1,100 m alt., same loc., *W. C. Steere, O. Mårtensson,* and *K. Holmen* 60–1215, July 23, 1960 (C); on dry rocky slope, 800 m alt., Feniak Lake, Delong Mts., 68°17′ N., 158°20′ W., *K. Holmen* and *O. Mårtensson* 61–140, July 31, 1961 (C).

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[1] Abbreviations for herbaria used in the citation of specimens are as follows: C—Universitetets Botaniske Museum København; CAN—National Museum of Canada, Ottawa; DAO—Dept. of Agriculture, Ottawa; DUKE—Duke University, Durham, N.C.; FH—Farlow Herbarium, Harvard University, Cambridge, Mass.; MICH—University of Michigan, Ann Arbor; NY—New York Botanical Garden; S-PA—Riksmuseets Paleobotaniska Avdelning, Stockholm; TENN—University of Tennessee, Knoxville; TRH—Kgl. Norske Videnskabers Selskab Museet, Trondheim. I am very grateful to the curators of the various herbaria for the generous loan of specimens.

NORTHWEST TERRITORIES, CANADA: Vicinity of Pangnirtung, Baffin Island, *V. C. Wynne-Edwards* 75, Sept. 3–5, 1953 (CAN, NY); in crevices of cliff near mine ventilating system, north of Labine Point, Port Radium, Great Bear Lake, *J. Kucyniak* 48–38, July 4, 1948 (MICH, as *E. ciliata*); on cliff near Labine Point, vicinity of El Dorado Mine, Port Radium, east end of McTavish Arm, Great Bear Lake, 66°05′ N., 118°02′ W., *W. C. Steere* 10117, July 4, 1948 (CAN, TENN, DUKE, as *E. ciliata*).

BRITISH COLUMBIA: In moist rock crevice, ca. 3,300 ft. alt., above Fort St. John (near Mile 106), 57°07′ N., 122°40′ W., *D. S. Correll* 11941, June 30, 1943 (MICH, as *E. ciliata*); on moist rock surface, ca. 4,000 ft. alt., head of Summit Lake, above Fort Nelson (near Mile 103), 58°38′ N., 124°40′ W., *D. S. Correll* 11993, July 18, 1943 (MICH, DUKE, as *E. ciliata*); on rock slide, Sliding Mountain, 53°09′ N., 121°29′ W., *F. M. Boas* 468, May 29, 1958 (CAN).

ALBERTA: On scree, 4,500 ft. alt., north side of Whistler Mountain, Jasper National Park, *C. D. Bird* 5053, Aug. 16, 1960 (CAN).

QUEBEC: On dry trap, mainland south of Cairn Island, Richmond Gulf, Hudson Bay, *J. Marr* M331, July 3, 1939 (MICH, NY, as *E. ciliata*); on diabase trap, same loc., *J. Marr* M356, July 6, 1939 (MICH, mixed with *E. rhaptocarpa;* NY, as *E. rhaptocarpa*); Seal Lake, Labrador, *A. P. Low,* Aug. 3, 1896 (CAN, NY, as *E. subbrevicolla*); Fort Chimo, Labrador, *A. P. Low,* Aug. 30, 1896 (CAN, NY, as *E. labradorica*): on bank of stream, 2 miles south of base, Fort Chimo area, *J. A. Calder* 2496, Aug. 10, 1948 (CAN, DAO).

Encalypta longicolla Bruch ex BSG is an exceedingly rare species only recently reported as new to North America. Persson and Gjaerevoll (1957) recorded it from three localities in Alaska. The species is known otherwise only from the Alps and the Jura Mountains of Europe, where it is a distinct calciphile of alpine and subalpine zones. The distribution is discussed and mapped in the paper by Persson and Gjaerevoll, who found that the ecological requirements in Alaska are similar to those in Europe, as evidenced not only by the substratum but also by the assemblage of associated calciphilous bryophytes.

I recently discovered a Canadian specimen of *E. longicolla* as an admixture in a collection from northern British Columbia made by Donovan S. Correll during a botanical exploration of the Alaska Highway in 1943. Two specimens of the same number (12086), originally named *E. rhaptocarpa* Schwaegr., contain at least thirteen different bryophytes in mixture: The one at the Farlow Herbarium consists mainly of *E. longicolla* and probably *E. rhaptocarpa*. (The capsules of the latter are old and worn, and no trace of the peristome could be found, but the spores are the large, warty type characterizing *E. rhaptocarpa* and *E. vulgaris,* the latter not likely to be found so far north.) The specimen at Duke University contains no *E. longicolla*. Other bryophytes present are essentially the

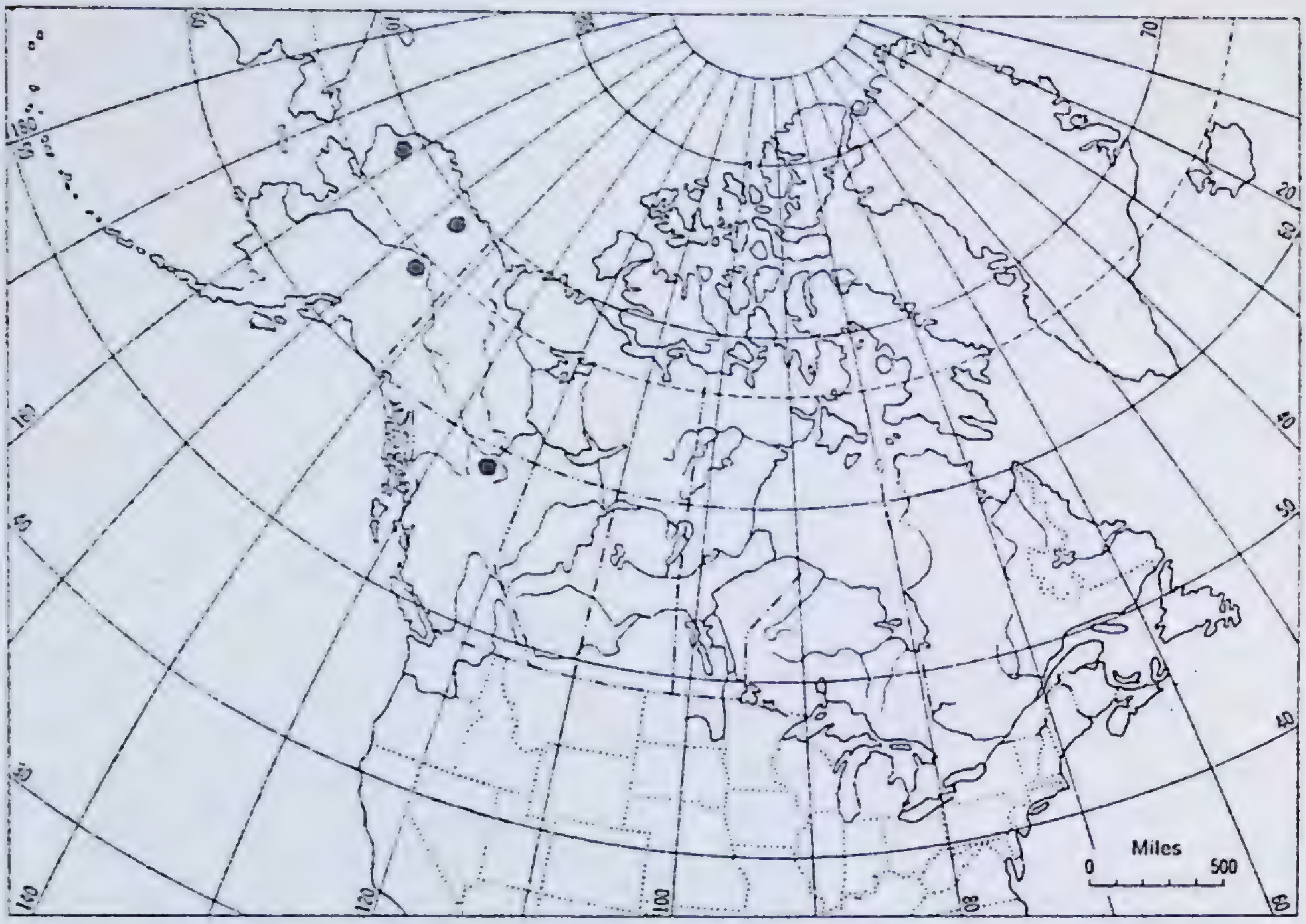

FIGURE 2. The North American distribution of *Encalypta longicolla*. The two northern Alaskan localities are included on the authority of Persson and Gjaerevoll (1957)

same in both specimens. An enumeration of them serves to emphasize the calcareous nature of the substratum: *Ditrichum flexicaule* (Schwaegr.) Hampe, *Pohlia cruda* (Hedw.) Lindb., *Mnium hymenophylloides* Hüb., *M. orthorhynchum* Brid., *Myurella julacea* (Schwaegr.) Myr., *Isopterygium pulchellum* (Hedw.) Jaeg., and *Blepharostoma trichophyllum* (L.) Dum., in addition to sterile and indeterminable plants of *Distichium, Bryum,* and *Brachythecium.* Such a community of bryophytes is very common in the Canadian Rocky Mountains, as in Alaska and the Yukon, and is typical of damp, shaded niches in calcareous situations, perhaps soil sheltered by rocks, on cliff ledges, or in small depressions of banks. In the White Mountains of Alaska, Gjaerevoll collected *E. longicolla* in a *Dryas punctata* heath with a very thin layer of humus on a limestone ridge; a number of the associated species were the same as those found with the British Columbia plants. The two other Alaskan specimens cited by Persson and Gjaerevoll were not available for study, and their ecological origins are not known, although they almost surely came from calcareous substrata.

In British Columbia and in Alaska, both *E. longicolla* and *E. brevicolla* have been found in the same general areas, and it can perhaps be inferred that they have similar ecological requirements. Dr. Correll also found *Oreas martiana* not far away in British Columbia; it is otherwise known from Alaska and Colorado, as well as the Alps. *Trematodon brevicollis,* with the same type of disjunction, has been found recently in southwestern Yukon and in Alaska in supposedly unglaciated mountainous areas. These and other rare bryophytes of similar disjunction have very likely survived the vicissitudes of the Pleistocene *in situ,* and it seems safe to predict that they will eventually be discovered in many other localities in the Canadian Rocky Mountains and the Brooks Range of Alaska, because of an abundance of calcareous habitats undisturbed by extensive glaciation.

Encalypta longicolla is very distinctive in habit and structure and can be recognized easily by the following features: Small gametophytes; leaves incurved-contorted when dry and so strongly concave as to appear linear; capsules with a well-developed neck shrivelled when dry and abundantly stomatose; peristome large in proportion to the size of the capsule and a rich purplish-red, the teeth irregularly divided into four linear, anastomosing divisions adherent to the segments of the endostome which are about the same length; very large and rather coarsely papillose spores. Previous descriptions indicate that the spores may reach a diameter of 100 μ or more, but I have not seen them greater than 73 μ. The neck of the capsule is certainly elongate and conspicuous, but not as long as the spore case or longer, as usually stated, but only about one-quarter to one-third of the total length of the urn. The capsule is usually smooth, but when dry and empty it may be irregularly furrowed. The essential features of the species are well illustrated in the *Bryologia Europæa* plate 202, reproduced here as Plate 1. Excellent illustrations also accompanied Bruch's original description.

A detailed description based on American specimens follows:

Encalypta longicolla Bruch, Abh. K. Bayer. Akad. Wiss., Math.-Phys. Cl. 1: 282. Pl. 10 (below). 1832.

Small plants, 2 to 6 mm high, in loose, dull green or brownish tufts. Stems forked, moderately reddish-tomentose. Leaves 2 to 2.5 mm long (including the awn), crowded, incurved-contorted, concave and thus appearing linear when dry, spreading and somewhat concave when moist, oblong, oblong-ovate or oblong-spatulate, acute, the lower leaves ending in a yellowish apiculus becoming progressively longer toward the stem tip as a hyaline or yellowish, smooth hair-point up to about 0.6 mm long; margins erect or ± incurved above, entire except for projecting papillae; costa strong, excurrent, ± rough at back; upper cells 10 to 13 μ wide, hexagonal, firm-walled, densely papillose on both surfaces, lower cells smooth, oblong, pale, and delicate with reddish walls thickened at the ends, narrower in about 4 to 6 rows at margins forming an indistinct border. Autoicous; paraphyses of both ♂ and ♀ inflorescences simple, filiform; perigonial buds several on one or more short branches below the perichaetial inflorescence, slender, the bracts ovate-lanceolate, acuminate and short-awned. Setae 5 to 13 mm long, becoming red or reddish-brown with age, ± twisted when dry. Urn of capsule 1.8 to 2.3 mm long (including the neck), erect, oblong-cylindric, smooth (often becoming irregularly furrowed with age), ±narrowed below the mouth when dry, with a conspicuous, wrinkled neck about 0.6 to 0.8 mm long and tapered to the seta; operculum about 1.8 mm long, erect, stoutly long-rostrate from a convex base; annulus of about two rows of small, subquadrate, thick-walled cells, persistent; exothecial cells short in a few rows below the mouth, laxly oblong below; stomata numerous, restricted to the neck, phaneropore; peristome double, inserted below the mouth, the teeth 275 to 360 μ high, purplish-red, smooth or weakly papillose, 16, each divided into about 4 irregular, linear, ± anastomosing strands held together by adherent endostome segments which are about as long as the teeth, delicate, pale yellow or reddish-yellow, irregular and often perforated and smooth or irregularly papillose. Spores ellipsoidal, 59 to 73 μ long, brown, densely roughened with blunt, rounded papillae mostly about 2 to 3 μ in diameter (but ranging from about 1.5 to 4.8 μ on the same spore). Calyptra 4.5 to 6 mm long, smooth or slightly roughened by very low, blunt projections near the tip, whitish-lacerate at base.

SPECIMENS EXAMINED

BRITISH COLUMBIA: On moist, bare soil, ca. 5,500 ft. alt., above timberline on a south-facing slope of a high moraine, vicinity of Summit Lake, above a small lake at Mile 104, Alaska Highway (above Fort Nelson), 58°38′ N., 124°40′ W., *D. S. Correll* 12086, July 26, 1943 (FH, as *E. rhaptocarpa*).

ALASKA: In *Dryas punctata* heath, limestone ridge, ca. 950 m alt., White Mts., Central Yukon District, *O. Gjaerevoll* 655, July 18, 1953 (TRH).

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BOGS AND FENS ON ATTAWAPISKAT RIVER, NORTHERN ONTARIO

By Hugo Sjörs[*]

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INTRODUCTION

The flat, sedimentary area west of James Bay and south to southwest of Hudson Bay is generally known as the Hudson Bay lowland. The interior of this lowland, which incidentally lies between the same parallels as the British Isles, still remains one of the least explored parts of Canada. It exceeds the latter in areal extension, but its population of a few thousand is probably less than that of any other land area of corresponding latitude and size.

Comparable climatic and biotic zones are found about 8 to 15 degrees of latitude farther north in Europe than in Eastern Canada. An area composed of the northern three-quarters of Finland (the four northern counties) and Norrbotten county (län) in Sweden would be comparable to the Hudson Bay lowland in total area, and roughly in extension of the various vegetational zones from main boreal to arctic or alpine but has a population of 1·9 million. About forty per cent of this part of Fennoscandia is productive land, chiefly forest, and about thirty per cent is peatland, the rest being unproductive woodland, bare rock, alpine barrens, and lakes. Comparative figures for the Hudson Bay lowland are lacking, but potentially productive land, at present covered by forest, can be estimated at a few per cent only, chiefly in the south; lakes and rivers probably occupy about five per cent; arctic, hemi-arctic, and coastal barrens one or two per cent; and peatland (including unproductive woodland, which is mainly on peat) probably accounts for about ninety per cent of the total area.

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Even if the mentioned North-Fennoscandian area corresponds well in zonal position, its winters are less severe, the spring arrives earlier, and in the southern part the summers are longer. A closer climatic similarity may be found in the more continental districts east of the White Sea. These parts of the U.S.S.R. also correspond more closely in geological and physiographic features, being low, flat, sedimentary, and traversed by large rivers. The percentage of peatland is moderate in the European part of the U.S.S.R. but very great east of the Urals, where the most extensive peatland is found east and west of the middle and lower Ob river (Galkina, 1956, p. 554). This territory with predominant peatland is about four times as large as the Hudson Bay lowland. Even though it is not completely covered by peatland, the total area of peatland must be considerably larger in W. Siberia.

The peatland in the Hudson Bay lowland may be estimated at about 30 million hectares (about 110,000 square miles), of which at least 80 per cent are in Ontario. The percentage of peatland in relation to total land area in the middle and northern parts of the Hudson Bay lowland is so close to 100 per cent that it could scarcely be higher anywhere in the world.

The interesting physiography of the Hudson Bay lowland provides an impetus to scientific investigation but has also been a hindrance to its exploration, particularly before it became accessible from the air. Though exploration started very early, it was long confined to the coast and rivers, and even modern air-borne investigation parties are strongly dependent on the waters that are deep and large enough for safe landing and take-off. Between the large waters, any travel is still extremely slow, at least during summer, when the spongy or muddy peatlands with their innumerable pools are unfrozen.

Apart from records by early explorers and geologists, there exist several modern surveys of the lowland, including an unpublished geographical thesis (McGill University, Montreal) by Coombs and a short published treatise on the landforms by the same author (1954). Earlier, Hanson and Smith (1950) described some of the types of patterned peatland and small lakes in connection with bird studies. Short notes on the coastal zonation have been published by Moir (1954). Floristic data have been summarized by Dutilly, Lepage, and Duman (1954). Although the latter work contains a wealth of information often obtained under difficult circumstances, it is far from complete even for the river courses followed by these botanists, e.g., the Attawapiskat River. Phytogeographical studies in the Manitoban part of the lowland have been undertaken by Ritchie (1957, 1960*c*).

During the last few years, phytogeographical researches in the lowland have been initiated by the National Herbarium of Ottawa under the leadership of Dr. A. E. Porsild. Dr. I. Hustich, Professor of Geography at Helsinki-Helsingfors, Mr. W. K. W. Baldwin of the National Herbarium, Ottawa, and the author have also taken part in these investigations. Hustich has published several papers on the area (1955, 1957*a* and *b*; the latter work being a phytogeographical survey in English). The author and his wife were working there about six weeks in the summer of 1957, concentrating on the problems offered by the peatlands. This is no small task in a landscape that is covered almost completely by peat. Only two areas were examined more closely. An introductory non-technical paper (Sjörs, 1959), a list of the bryophytes (Persson and Sjörs, 1960), and a description of the more northern area, near Hawley Lake (Sjörs, 1961*b*), have been published. The present paper deals with the more southern area, on the middle Attawapiskat River, which was studied for nearly four weeks in July 1957 by a team of four.

Acknowledgments

With his vast experience, Porsild was a most competent and stimulating leader of the party. Besides his floristic and general phytogeographical study and much care devoted to practical considerations, he found time to discuss and work on the problems of peatland ecology and development, in which he shared our interest. He has also determined or checked the vascular species either in the field or on collected specimens, and has revised the manuscript very carefully. Baldwin was also extremely helpful in this study. My wife did most of the notetaking and all the pH determinations. She also assisted in transect recording, soil study, and peat-borings.

In addition to the co-operation within the team, another factor that added much to the efficiency was the careful selection of the area of investigation. This was a result of observation during previous flights and study of air photographs by Porsild, which proved to be essential in this area of very poor access except along the large rivers.

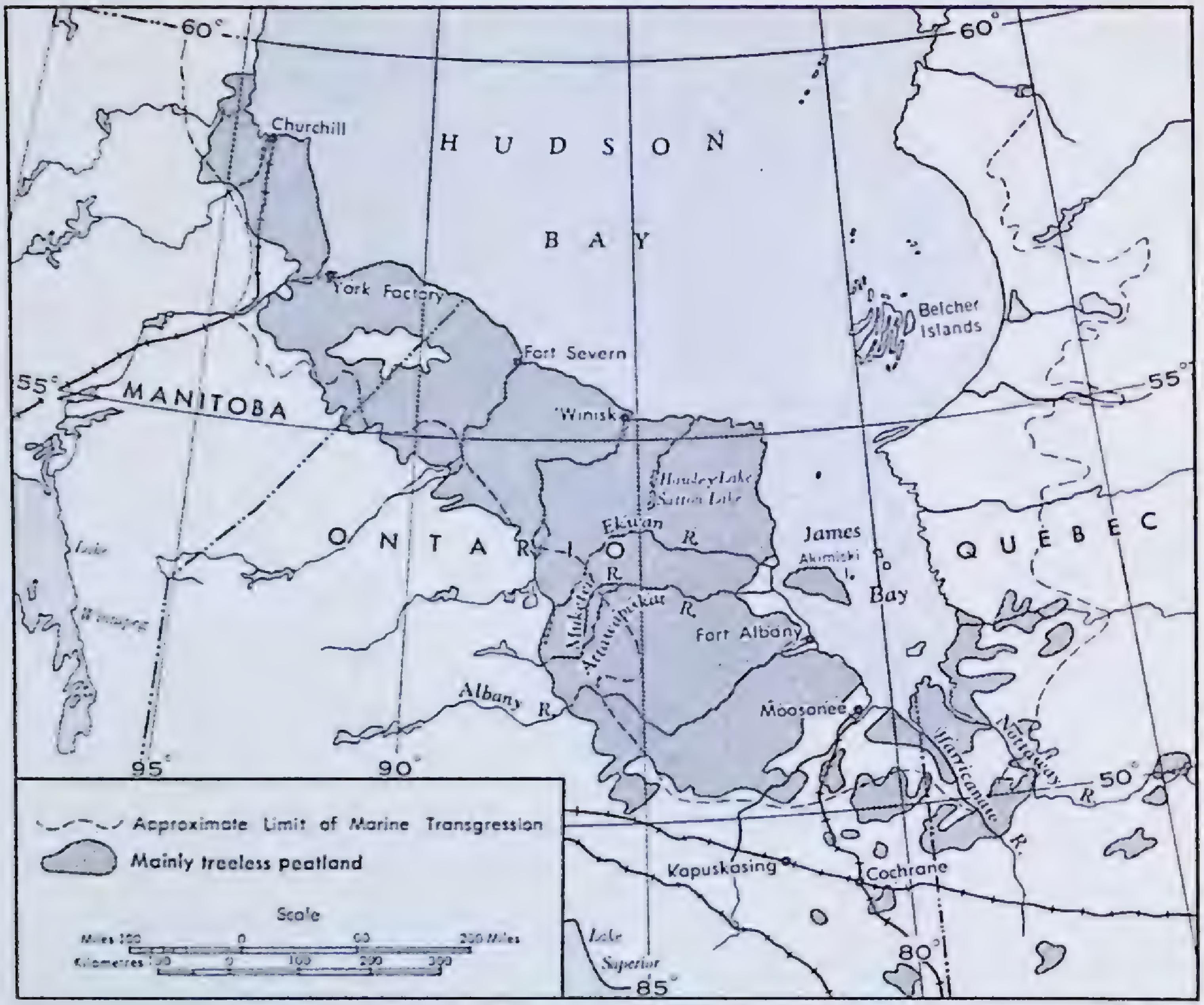
Invaluable collaboration was given by the Ontario Department of Lands and Forests, which provided air transportation to and from the campsites. We owe special thanks to our experienced and most helpful pilot, Mr. Tommy Cooke, and to his crewman and mechanic, Mr. George Wood.

The author is sincerely grateful to the Arctic Institute of North America for a generous grant from the Banting Fund, and to the National Museum of Canada, in particular for additional financial support and for the use of field equipment.

DISTRICT OF INVESTIGATION

Physiography

For a more comprehensive account of the physiography and phytogeography of the Hudson Bay lowland as a whole, the reader is referred to the works already cited (p. 46). Nearly the entire lowland rests on extremely flat, sedimentary, chiefly Palaeozoic rocks, which have never been appreciably tilted or folded. The gradient is considered to be only about four feet to the mile on an average but is of course somewhat variable. The general direction of the slope varies from northern to eastern, and even southeastern. The large rivers all originate in the Precambrian Shield south or west of the sedimentary lowland, although Ekwan River drains only an insignificant area of the Precambrian. Attawapiskat River, after entering the lowland, changes direction from east to north-northeast. Near its junction with Muketei River, which in its lowermost course runs southeast, the

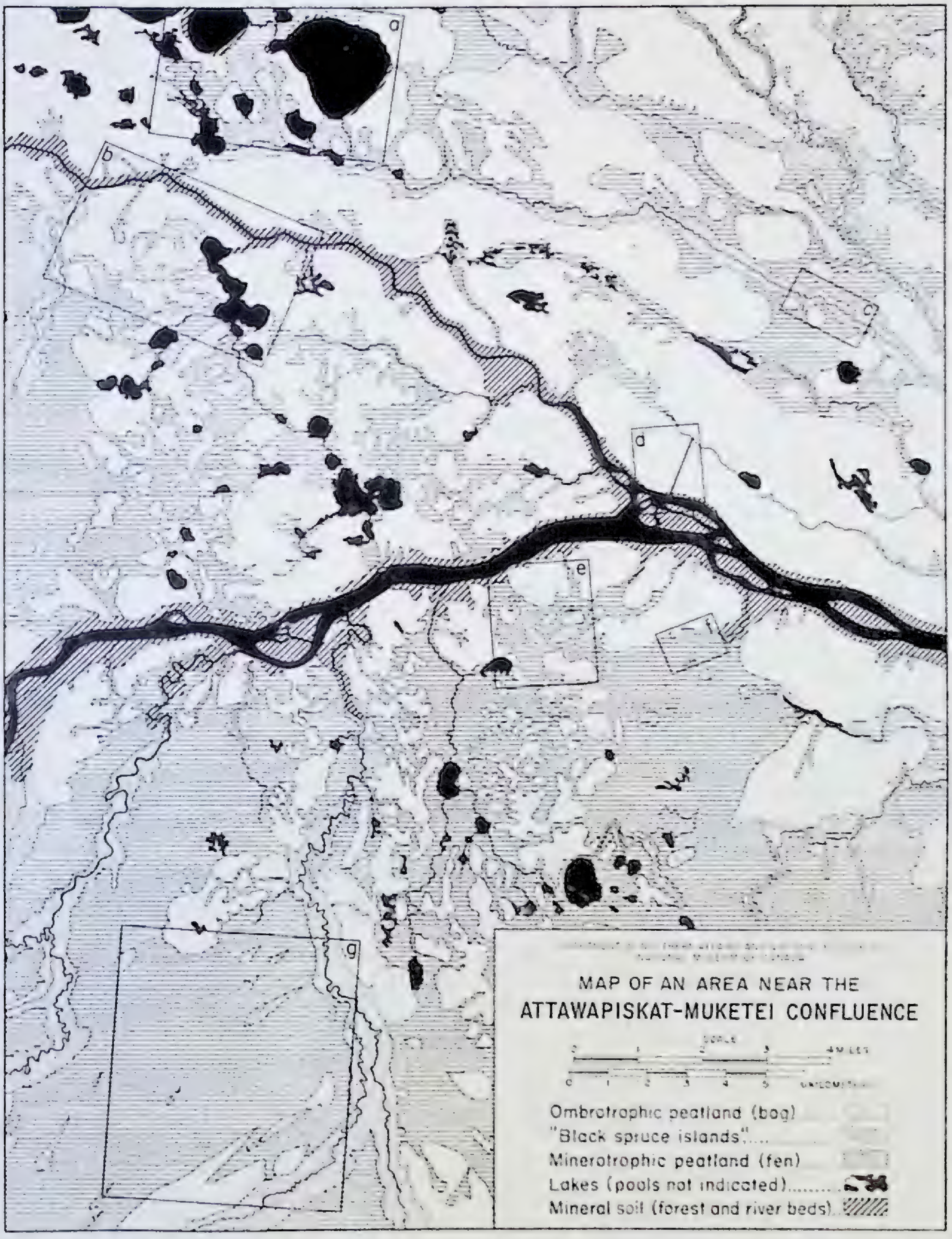


H.E. Mindak

TEXT FIGURE 1. Sketch map of the Hudson Bay lowland showing extent of open peatland (bog and fen, excepting largely wooded peat areas) and approximate limit of marine transgression. Area of investigation at Muketei-Attawapiskat confluence near centre of map. Based on the 1958 Glacial Map of Canada. —*From* ARCTIC *12, No. 1, 1959*

Attawapiskat trends to the east or even east-southeast. This part of the river system was formed gradually, as the land emerged from the sea in postglacial time. The highest former coastal level or "marine limit" is situated upstream from the confluence (Text Fig. 1). The Attawapiskat broadens considerably below the junction, where several streamlined islands occur in the river. They are often suggestive of huge but low flat-irons. Further downstream the river branches repeatedly. Some ancient river channels and ox-bows have become disconnected from the present channels and are partly overgrown by deep-green masses of peat-forming vegetation.

The large rivers have cut through marine clay and clayey glacial till, forming high banks on both sides, but there are no true river valleys. North of the Attawapiskat, the slope is not at all towards the river but parallel to it, as shown by the direction of several small streams (Text Fig. 2). To the south of it, the slope direction is more variable; here, too, it parallels the river for long stretches.


a
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MAP OF AN AREA NEAR THE
ATTAWAPISKAT-MUKETEI CONFLUENCE
0
1
2
3
4 MILES
0
1
2
3
4
5
Ombrotrophic peatland (bog)
"Black spruce islands"....
Minerotrophic peatland (fen)
Lakes (pools not indicated)........
Mineral soil (forest and river beds)..

Text Figure 2. Distribution of ombrotrophic and minerotrophic peatland, etc., in the investigated area. Based on R.C.A.F. air photos. The framed areas are shown magnified on the following plates: (*a*) Plate XXVIA; (*b*) Plate XXVIB; (*c*) Plate XXI; (*d*) Plate VIII, *see also* Colour Plates IIIA, IVA, Text Figs. 4, 6, and 7; (*e*) Plate XV; (*f*) Plate II; (*g*) Plate VII

The underlying bed-rock consists of limestones, calcareous sandstones, and so forth, of Silurian age. Only few exposures of bed-rock, however, were seen along the rivers, and none downstream from the junction, for almost everywhere the river banks are cut into glacial till. The extent to which this till is covered by marine clay is not easily observed, for the till is also very clayey and, like the marine clay, highly calcareous. Marine shells washed from the clay were seen frequently. Although few boulders are visible in freshly exposed till, they accumulate as the silt and clay fractions are washed away, and the river-bed is formed by a smoothed pavement of medium-sized boulders, with few larger erratics. Areas of considerable accumulation, chiefly of fine sand and calcareous silt, alternate with eroded shores along the river banks and on the islands. The accumulation banks are overgrown by dense willow thickets, formed by numerous species of *Salix* and in the higher parts other shrubs also. The thickets contribute considerably to the accumulation of silt during spring floods. The only tree that occurs on the river banks within reach of normal high water is balsam poplar (*Populus balsamifera*), in most places only as saplings, but on some of the islands as a distinct marginal wooded belt below the white spruce forest.

Nearly everywhere along high river banks and on islands, a narrow fringe of tall white spruce (*Picea glauca*), with rich under-vegetation (*see* Transect, p. 114), grows on alluvial soil, which is flooded only exceptionally as a result of ice-jams; this flooding causes deposition of large amounts of calcareous silt (*see* Sjörs, 1959, p. 7). Some mineral terraces seem to reach above even the highest floods. Balsam fir (*Abies balsamifera*), white birch (*Betula papyrifera*), aspen (*Populus tremuloides*), and balsam poplar are also found in this zone. Here and there the white spruce is replaced by tall, vigorous aspen; these sites are probably old local burns. The riverside vegetation will not be dealt with further in this paper, as the records are intended for a separate publication.

A short distance back from the river, white spruce gives way to black spruce (*Picea mariana*), and the humus cover normally becomes thicker and more peaty. The under-vegetation is poor in species but varies a good deal. The black spruce muskeg, a term that refers to the moist, peat-forming types, is mostly confined to marginal parts of peatland areas. It usually passes into open peatland at a variable distance from the river but may recur near smaller streams and brooks. (Regarding "black spruce islands," *see* pp. 107 to 114.)

Clay soils are exposed only along the large and medium-sized rivers. Elsewhere, mineral soil is always covered by organic deposits, either mor (forest humus) or, much more frequently, peat. The average depth of the peats is unknown, but deposits more than ten feet deep may be found in the open peatland, whereas those of the drier and more firm but still peaty black spruce muskeg are doubtless much shallower.

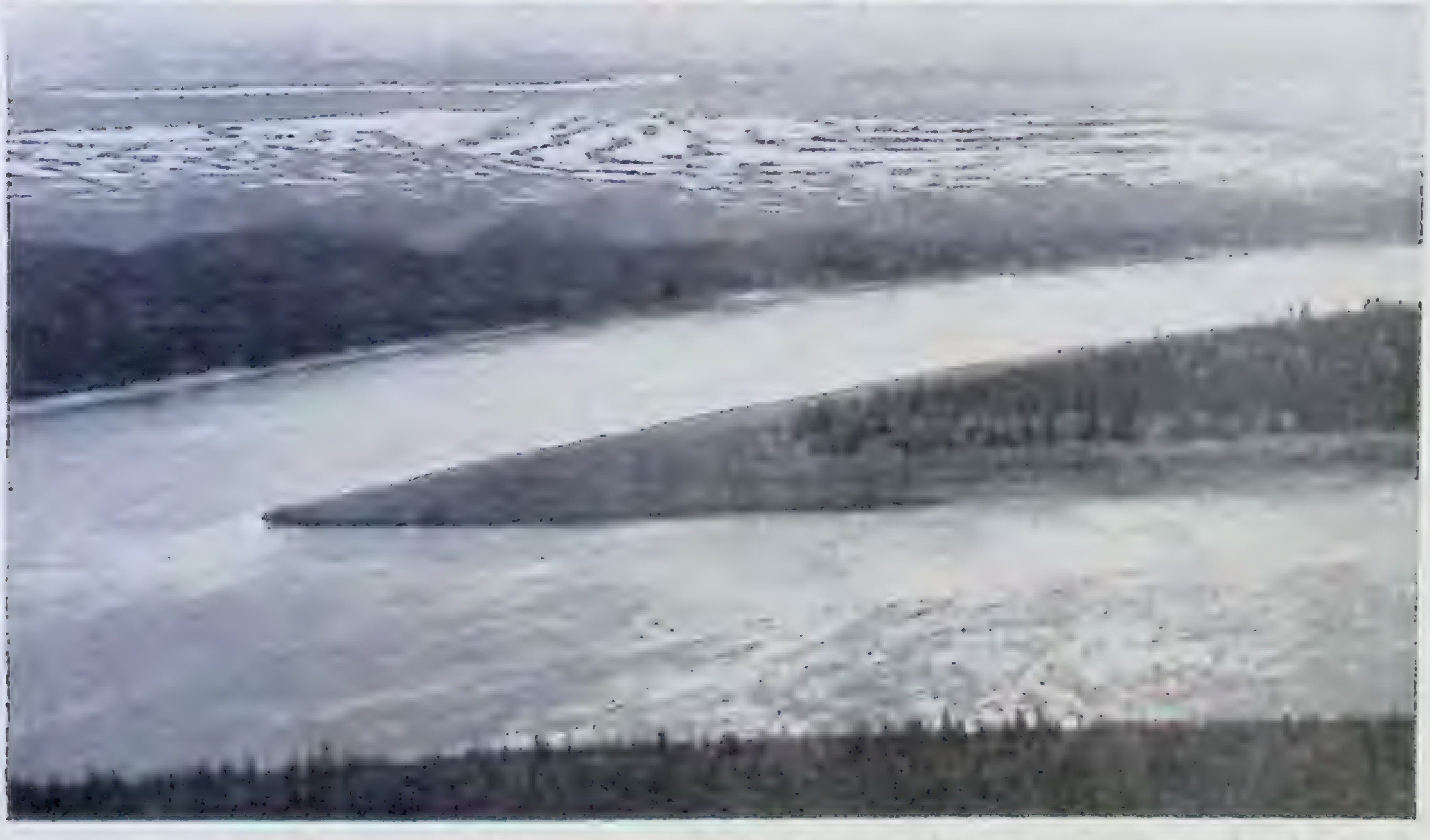
In the central part of the Hudson Bay lowland—the Muskeg and Small Lake Zone of Coombs (1954, p. 6)—peat covers all mineral soil, except very narrow strips along the large and medium-sized rivers and a few exposed eskers, and, near the rising coast, also former beach ridges that have not yet been buried in the peat. Lakes are rare near the coast, but in most parts of the interior country, rivers, lakes, and ponds cover about three per cent (according to Coombs); the fraction of mineral ground is negligible. In certain areas, called "Small Lake Areas" by Coombs or "Pothole Muskeg" by Hanson and Smith (1950, p. 92), the percentage of open water is much higher (10 to 50 per cent, according to Coombs, but over thirty per cent is exceptional). Such areas are mostly confined to the major water divides, where the slope is insignificant. Certain "pothole" areas where islets of peat-forming vegetation occur in the lakes are important as breeding sites for Canada geese of the Mississippi flyway (Hanson and Smith, op. cit., pp. 96–101).

The areal percentage of wooded peatland, including black spruce muskeg and tamarack (*Larix laricina*) swamps, is always much less than that of open (more or less treeless) peatland. The dominance of open peatland over wooded is greatest in the northern and coastal parts of the lowland. In the southernmost part of the lowland, the percentage of wooded peatland is considerable (Hustich 1955, 1957*b*, pp. 35, 41), and mineral soils occur to some extent, but even there, as open peatland is usually dominant, the expression "Dry Zone" used by Coombs becomes significant only in a relative sense, when compared with the so-called "water desert," which comprises the central and northern parts.

CLIMATE

According to Hustich (1957*b*, p. 5), the climate of the Hudson Bay lowland ranges "from temperate conditions in the southwesternmost part of

PLATE I



Southward view across Attawapiskat River 5 miles downstream from the Muketei confluence (downstream end of right island on map, Text Fig. 3, p. 68). White spruce on banks and in centre of island. The tall shrubs are balsam poplar, and those near the water's edge chiefly willows. Across the river, an up-domed, ombrotrophic bog with numerous very large bog-pools, some of them 500 m long.
—*Photo G. Sjörs*

the area, to more or less arctic conditions at Cape Henrietta Maria and Fort Churchill." In an unpublished report to the Arctic Institute of North America, Hustich emphasizes the progressively and rapidly increasing temperature (particularly during early summer) when travelling inland from Fort Severn on the north coast.

The summer temperature is certainly much higher around the middle Attawapiskat River than on the coast of Hudson Bay to the north. Also it is no doubt considerably more favourable than near James Bay, to the east and even southeast. Air temperatures exceeding 90°F (+32°C) were recorded repeatedly by us during July, with a maximum of 95°F (+35°C). The fast growth and the tallness of aspen and white spruce on favourable soils also indicate an adequate supply of heat during the growth season, which, moreover, begins earlier than on the coast.

Moosonee, near the south end of James Bay, is the only weather station in the area with long period records (Chapman, 1953; Rowe, 1955). Here a mean July temperature of 61°F (about +16°C) is recorded, which is exactly the same as the mean July temperature of most of the lowland in Sweden and Finland. The July isotherms roughly parallel the Hudson Bay coast (Robinson, 1954, p. 37; Chapman, 1953, p. 49). No data are known from the area of investigation on the middle Attawapiskat River, which is about 120 miles (200 km) inland. It seems likely that early and middle summer is slightly warmer here than at Moosonee, owing to the inland situation. These two localities, in particular the area of investigation, should be regarded as temperate (main boreal) rather than subarctic regarding summer temperature conditions, as well as vegetation.

As a measure of the length of the growth season, the number of days with a mean temperature over + 5.5°C (42°F) is often given. This number is 143 at Moosonee (Rowe, 1959, p. 65). The average growth season begins on the 18th of May and ends in the first week of October at Moosonee (possibly both dates are slightly earlier on the middle Attawapiskat River). The length of the growth period at Moosonee is almost identical with that of the well-populated European areas of agriculture, forestry, and industry on the northern shores of the Gulf of Bothnia, as, for instance, near the towns of Luleå, Haparanda, and Torneå (Tornio). The summer maximum is even slightly higher at Moosonee. Admittedly the Hudson Bay lowland winter temperatures are much lower. Also, in spring and summer the hours of daylight are fewer because of the lower latitude. The lag between longest day and temperature maximum is about one week more than in Scandinavia. Whereas the period of maximum growth in trees coincides with the light maximum in northern Fennoscandia, less of the latter period is available for active growth in the Hudson Bay area because of the late arrival of summer. This seems to be most important in the northern and coastal areas and may even check wood production in trees to a considerable extent in the latter regions, which belong to the "subarctic" and "hemi-arctic" zones (*see* below).

The annual precipitation may be very roughly estimated at about 20 inches (500 mm), of which probably about one-third falls as snow.

According to Brown (1960, p. 169) the Attawapiskat River region is well outside the distribution area where permafrost is continuous and on the south rim of discontinuous permafrost, which is almost certainly restricted to the distinct "black spruce islands" in the peatlands (p. 110). The frost still present, in July, in certain other black spruce stands, and in some bog hummocks, is seasonal and disappears in late summer.

REGIONAL POSITION

In Halliday's regional forest classification (1937), the northern Hudson Bay lowland belongs in the Northern Transition Section, and the southern parts in the Coastal Plain Section, the boundary being drawn a short distance north of and parallel to Attawapiskat River. Our area thus belongs in the Coastal Plains Section, which was called "the Western James Bay Section" by Hustich (1949). Both sections are rather heterogeneous from a zonal point of view. In the recent revision by Rowe (1959; *see also* MacLean and Baldwin, 1959, p. 18), the whole lowland is shown as the Hudson Bay Lowlands Section (Rowe, op. cit., p. 15), except the northern coast, which is part of the Forest Tundra Section (p. 35).

Hustich (1957*b*), who has dealt in considerable detail with the phytogeography of the area, does not delimit or define the phytogeographical or forest-geographical regions or zones within it. His descriptions of vegetation and his tentative maps of the distribution of tree species show that several different regions exist in the lowland. Apparently the few data available on forest growth and composition of vegetation, and particularly the sparseness of well-developed forest, have discouraged scientists from a further refinement of zonal subdivisions. However, forest zones can be recognized even when very little forest is actually present.

The extensive non-forested peatland in the lowland should not be confused with open areas due to development of nearly treeless tundra found near the arctic treeline. The designation of the northern section as "an edaphic forest tundra" (Hustich, 1957*b*, p. 16) is therefore misleading, because, as Hustich rightly states, "it is not the climate itself which accounts for the scarcity of the forest, but the edaphic condition prevailing there" (loc. cit.). These edaphic conditions promote peatland development, not formation of tundra.

Zonal subdivisions have been worked out in more detail for Quebec-Labrador and Manitoba than for northern Ontario. Although the terminology of different authors is not the same, the regions or zones proposed are actually very similar, even when Quebec-Labrador is compared with Manitoba, and obviously the same regions occur in northern Ontario. Hustich's concepts of tundra, forest tundra, "taiga," and "southern spruce forest" regions (1949, 1951) in Labrador were first adopted for Manitoba by Ritchie (1956*a*), but in Ritchie, 1959 (p. 6) the "taiga" was re-named "subarctic forest." Ritchie has recently (1960*b*, 1962) discussed the major zonation in northern Manitoba more comprehensively but has arrived at different zones of vegetation in the Shield and Lowland sections. The lowland zones in northern Manitoba were distinguished according to physiognomy of vegetation cover and surface pattern but unfortunately are of limited use in the Ontario section of the lowland, which is largely different in these respects (cf. Coombs, 1954). The difference seems in part to be due to the much greater extension of permafrost in Manitoba (Brown, 1960).

For Labrador-Quebec, Hare (1950, 1954; Hare & Taylor, 1956) used the terms tundra, forest tundra (ecotone), open boreal woodland, and main boreal forest. The latter two subdivisions are termed "woodland or parkland sub-zone," and "forest sub-zone" (of the "boreal formation") in Hare's recent work (1959). Also for Labrador-Quebec, Rousseau (1952) distinguished an arctic, a "hemi-arctic," a subarctic, and a temperate zone. In these zones the dominant "habitats" (i.e., vegetation types) are tundra, forest tundra, "taiga" or subarctic "parkland," and temperate coniferous forest respectively. The boundaries proposed for corresponding subdivisions are much the same in Hustich's, Rousseau's, Rowe's, and Hare's works (more detailed in Rowe, 1959, and Hare, 1959). In the present connection it should be observed that the boundary between the open boreal woodland and the main boreal forest according to Hare (1950) lies farther north in the James Bay area than the corresponding line as shown on maps by other authors.

This is not the place for a full discussion of the vegetation regions, or biotic regions (Sjörs, 1955, p. 163), in northeastern Canada. Numerous authors (besides those already mentioned, e.g., Marie-Victorin, 1935; Raymond, 1950; Baldwin, 1953, 1958; Dutilly, Lepage, and Duman, 1954; Scoggan, 1957) have given important contributions to the knowledge of regional zonation here.

The present author will use the following terms for the zonal subdivisions of the boreal forest region: hemi-arctic woodland tundra region, subarctic woodland region, and main boreal forest region. These terms seem to be applicable for most of the boreal zone, in North America as well as in Eurasia (cf. below, and Sjörs, 1962).

In a tract of land where forest sites are subordinate, it is important to emphasize that a "forest region" is not just forest; thus, for instance, "subarctic woodland region" is more correct than "subarctic woodland." Regions, if extended more or less around the globe, become zones. For a particular sector of the globe one should use "region" if the conditions discussed are not of world-wide significance.

In the Hudson Bay lowland, only small coastal areas near Cape Henrietta Maria and near Churchill, Manitoba, are more or less arctic (*see* map of polar limit of conifers, Hustich, 1957*b*, p. 27). The northern part of the James Bay coast and the Hudson Bay coast belong to a very narrow hemi-arctic woodland tundra region, termed "la zone de transition" (toward the Arctic) by Dutilly, Lepage, and Duman (1954, p. 3) and shown on Rowe's map (1959) as "forest-tundra section." Near Winisk, only the seashore and the mouth of Winisk River are in this hemi-arctic region. Suitable sites near the Hudson Bay Company Post at Winisk are well wooded, particularly on drained soils, and thus belong to the more southern subarctic woodland region. Conditions near Fort Severn (Hustich, unpublished report to the Arctic Institute of North America) are very similar. The middle and southern parts of the west coast of James Bay are distinctly subarctic, for instance, at Fort Albany and Attawapiskat Post. At least part of Akimiski Island "possède également une étendue appréciable en forêt" (Dutilly, Lepage, and Duman, 1958, p. 10). Also the areas near Hawley Lake and Sutton Lake are typically subarctic and occupy a central position in the subarctic woodland region (Sjörs, 1916*b*, p. 6).

Between Sutton Lake and the Muketei-Attawapiskat confluence, the transition from the subarctic woodland region to the main boreal forest region is gradual, but observations from the air indicate that the boundary may be drawn as far north as the middle Ekwan River and passes southeast to the vicinity of the mouth of Moose River. At Renison on the lower Moose River, forest growth (Hustich, 1955) is slightly superior to that near the Muketei-Attawapiskat confluence; both areas are thus well within the main boreal forest region. According to Hustich (unpublished report), growth conditions are main boreal rather than subarctic near Big Trout Lake. This lake is on the Precambrian Shield, at about 230 m above sea-level, and only 2 degrees to the south of the coastal woodland tundra region at Fort Severn. According to Ritchie (1956*a*, p. 555), Tod Lake and MacBride Lake in Manitoba have a similar regional position as Big Trout Lake. The main boreal-subarctic boundary probably passes near Gillam, Manitoba (Ritchie, 1960*b*). Judging from Baldwin's description (1953), subarctic conditions are found on the northern part of Reindeer Lake on the Manitoba-Saskatchewan border.

The subarctic woodland region and the main boreal forest region in Canada correspond fairly well to the Northern and Central taiga regions distinguished by Russian authors (*see* the condensed regional map inserted into the Geobotanical Map of the U.S.S.R. by Lavrenko and Sochava, 1954, also reproduced in Sotchava, 1954, and in Tikhomirov, 1960, p. 822). The regional position of the Attawapiskat River locality would correspond to the northernmost parts of the Central taiga, for instance on the lower Dvina River, or near the junction of Ob and Irtysh rivers.

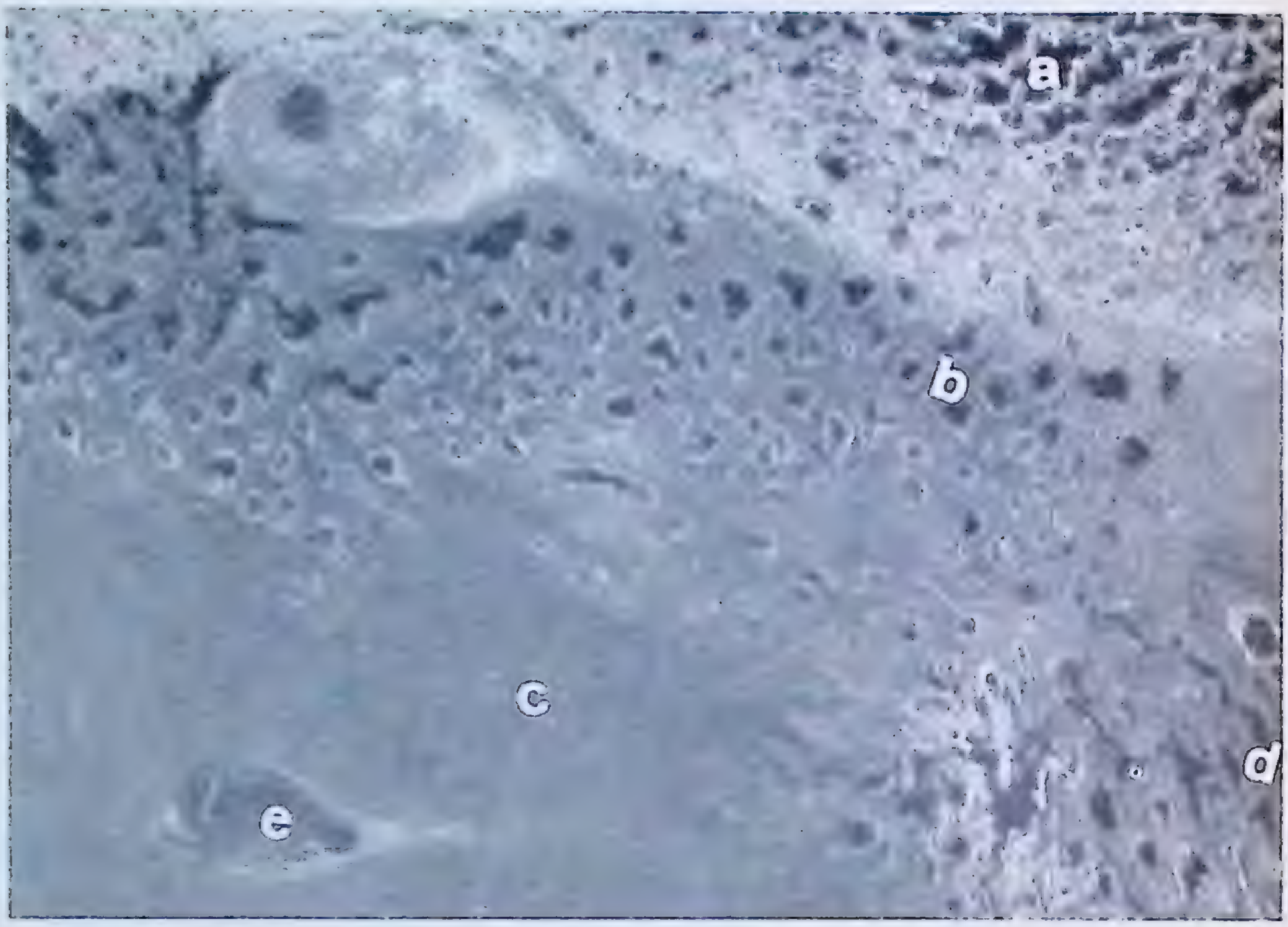
Owing to less continental conditions a Fennoscandian parallel is not easily located, but the northern Bothnian region corresponds fairly well. The greatest similarity in regard to peatland morphology is with Ostrobottnia (Österbotten, Pohjanmaa) according to Ruuhijärvi (1960; map p. 255), but also part of northern Sweden and the central Swedish uplands are fairly comparable (Malmström, 1923: Sjörs, 1948: Lundqvist, 1951*b*).

TROPHIC TYPES IN PEATLAND

Ombrotrophy and Minerotrophy

Among the factors affecting peatland vegetation, the supply of mineral nutrients has long been recognized as extremely important. It is well known that some peatlands called bogs (in the most restricted sense of the word) derive their entire water supply from precipitation, whereas other peatland areas, termed fens (in the corresponding wide sense), are under intermittent or more or less constant influence of water that has been in contact with mineral soil. In the long run, the formation of peat, not only fen peat, but also bog peat, even of the poorest type in regard to plant nutrients (ash content only 1 to 2 per cent by weight), results in a withdrawal of significant quantities of minerals from the ecosystem. Unlike vegetation on mineral soil, peatland vegetation is therefore dependent on mineral nutrients reaching the ecosystem from outside, either exclusively

PLATE II



Vertical view of area *f*, Text Fig. 2 (p. 49), 2 miles south of river confluence. (*a*) Ombrotrophic bog with small pools. (*b*) Rich (calcareous) minerotrophic fen sloping eastward, with scattered pools and a narrow pattern of ridges and "flarks" at right angles to slope. Note sharp boundary between (*a*) and (*b*). (*c*) Similar minerotrophic fen with micro-pattern barely visible on original photo, and lacking pools. (*d*) Source of a brook. (*e*) Black spruce island, with ombrotrophic "tail" pointing downslope.

—*Photo by R.C.A.F.*

with precipitation and dust, or with mineral soil water in addition. When dynamic equilibrium is reached, mineral nutrients deposited in new-formed peat equal the access from outside minus the loss in run-off.

If the supply of mineral soil water ceases, the content of mineral nutrients in new-formed peat will diminish, as will the loss of minerals with the run-off water. The vegetation cover will change, adapting itself to deficiency in nearly all minerals and to an ionic composition of the substrate that is closely governed by (but not identical with) that of the precipitation reaching it. These conditions have been termed *ombrotrophic* (i.e., rain-nourished; Du Rietz, 1954*b*) in contradistinction to *minerotrophic*. Earlier the word "ombrogenous" was in current use also for the trophic conditions, but this word actually refers to conditions of peat formation; for plant nutrient conditions, the new term "ombrotrophic" is preferable. It has recently been adopted as a basic ecological concept in the study of peatlands in northern Finland also (Ruuhijärvi, 1960).

Even if ombrotrophic peatland vegetation receives nutrients only from rain, snow, dust, and perhaps minute quantities of ammonia in the air, the peat which is its substrate contains these nutrients in larger concentrations than those of the original precipitation water, and in different proportions. Peat is a selective adsorbent of ions (notably cations) and will give off hydrogen ions in exchange for metal ions, particularly the bivalent ones (most important Ca^{2+} and Mg^{2+}). This process also reaches a dynamic equilibrium. In most of the investigated, purely ombrotrophic sites in the Swedish inland (cf. Sjörs 1961*a*), about 10 per cent of the cation exchange capacity is covered by bivalent metal ions, a few per cent by monovalent ones (K^+ and Na^+), and almost all the rest by H^+.

The water enclosed in the peat will differ from precipitation, in particular with respect to hydrogen ions. Thus it will be much more acid, but it is a matter of dispute what acids it contains. Sulphate ions, received from rain or formed by oxidation of sulphur compounds, and in certain cases even free sulphuric acid, are regarded as an important cause of acidity by Gorham (1956*b*, 1958, etc.). Ramaut (1954, 1955*a* and *b*) holds the view that organic acids (possibly succinic acid) are excreted by living *Sphagnum*, in addition to the adsorptive process mentioned (recently studied by Anschütz and Gessner, 1954). This would give an acceptable explanation of certain phenomena observed in nature, particularly the greater acidity of *Sphagnum* carpets, also in cases where water from mineral soil is received, and explain the fact that *Sphagnum* will never cease entirely to give off acid on repeated washing with distilled water (Kivinen, 1932, p. 92). In any case, ombrotrophic sites are always acid, but if the quantity of peat and *Sphagnum* is small in relation to the amount of water, the acidity will be less marked. This is, for instance, the case with the very large bog-pools in the bogs near Attawapiskat River, which may even be considered reservoirs of atmospheric water.

According to Pearsall (1938, 1941; Pearsall & Mortimer, 1939; Pearsall & Lind, 1941), the acidity is greater under oxidizing than under reducing conditions. Oxygen is scarce or absent one to a few inches below the water table in most peatland (Malmström, 1923).

Data on the ionic conditions in ombrotrophic and minerotrophic peatland are found in numerous works. Among more recent ones the following should be mentioned: Kotilainen, 1928; Kivinen, 1933, 1934, 1935; Thunmark, 1942; Mattson, Sandberg & Terning, 1944; Sjörs, 1946, 1948, 1952, 1961*a*; Witting, 1947, 1948, 1949; Du Rietz, 1950*a*, *b*, *c*; Gorham, 1952, 1953, 1956*a* and *b*, 1957, 1958, 1961; Puustjärvi, 1952, 1956, 1957; Mattson & Koutler-Andersson, 1954; Malmer & Sjörs, 1955; Gore & Allen, 1956; Kaila & Kivekäs, 1956; Kivekäs & Kaila, 1957; Malmer, 1958, 1962*a* and *b*; Newbould, 1960; Å. Persson, 1962.

Ombrotrophic conditions, being extreme, do not vary much in a given district. Minerotrophic conditions, on the other hand, are highly variable. Precipitation dilutes the flow of minerotrophic water to a variable degree. Certain parts of the minerotrophic peatland also receive, at intervals, the surplus of ombrotrophic water from near-by bogs. The flow of minerotrophic water may be weak or strong; a weak flow will be more effectively diluted by precipitation or by flow of water from ombrotrophic bogs. Last but not least, mineral soils differ in composition, and so does, therefore, the mineral soil water that reaches the minerotrophic peatland. Thus a very coarse Precambrian (silicious) till, or a glacifluvial deposit of gravel

TABLE 1. *Chemical properties of water samples*

No.	Site type	Date, July 1957	pH		Conductivity lab.		Loss on ign. mg/l	Residue on ign. mg/l	Fe mg/l	Ions, as parts per million (mg/l)						
			field	lab.	obs.	red.				Ca^{2+}	Mg^{2+}	Na^{+}	K^{+}	Cl^{-}	SO_4^{2-}	HCO_3^{-}
1	Bog-pool............	23	4.5	4.6	19	11	22	2	0.02	0.5	0.2	0.3	0.1	1.2	1.1	0
2	"Seepage"..........	22	4.8	4.75	22	16	62	7	0.05	1.7	0.5	0.3	0.1	2.0	n.d.	0
3	"Fen flark".........	20	7.1	6.8	48	48	73	37	0.57	8.9	1.8	0.9	0.3	2.4	n.d.	24.1
4	River...............	23	8.0	7.5	85	85	38	48	0.09	15.8	2.8	0.6	0.4	1.2	0.7	56.3

Analyses by Dept. of Mines and Technical Surveys, Mines Branch, Industrial Waters section, Ottawa, Ont.

Specific conductivity is expressed in inverted ohms $.10^{-6}$, at +20°C. Reduced conductivity: the conductivity of H^{+}, calculated from pH (lab.), has been subtracted (Sjörs, 1952, p. 246). Ign. = ignition of residue on evaporation, at about +550°C. Fe is total iron. Manganese, nitrate, phosphate, silica: amounts beyond sensitivity of analysis. n.d. = not determined.

1. Bog-pool No. 2 in Transect I. Ombrotrophic bog at Attawapiskat-Muketei confluence.
2. Small, shallow pool in "seepage," presumably faintly minerotrophic, with "poor fen" vegetation (p. 96). S. side of Attawapiskat River 3 miles downstream. Table 3, No. 86.
3. "Rich fen" above *Thuja* site, "flark," minerotrophic. S. side of Attawapiskat River, 2 miles upstream. Table 4, No. 82.
4. Attawapiskat River just below confluence but out of reach of water from Muketei River.

or sand, gives off fewer mineral ions than does a fine-textured till, or a soil derived from fine-grained water sediments, or, finally, a calcareous soil.

The degree of minerotrophy within those peatland habitats is more or less correlated with types of vegetation, e.g., the "poor fen" and "rich fen" of Du Rietz (1949); *see* further p. 60. Some of the papers quoted above tend to show that this difference, although originally brought about by the water, is more definitely related to the chemical properties of the peat than to differences in ionic concentrations in the minerotrophic fen water. The present author (Sjörs, 1946, 1952) was able to demonstrate that intermediate fen vegetation, and even "moderately rich" fen vegetation, could develop with very dilute minerotrophic water, if the acidity was moderate. Such conditions occur in northern Fennoscandian non-calcareous areas similar to some Precambrian parts of Canada. However, the prevailing type of minerotrophic fen in these areas, the "poor fen," is acid and its flora poor in species. *Sphagnum* is usually so abundant that the poor fen has frequently been classified as bog, although not ombrotrophic.

In the Palaeozoic Hudson Bay lowland, however, mineral soil everywhere is calcareous, and degrees of minerotrophic influence will mainly imply degrees of influence of lime. This is evident from the great variation in calcium ions in Table 1, other ions varying much less.

In this calcareous region, "poor fen" will generally be confined to areas where the influence of minerotrophy is barely noticeable and where the larger part of the water is derived from ombrotrophic areas and thus retains much of its acidity.

In the absence of non-acid minerotrophic water of low Ca^{2+} content, "rich fen" vegetation, on the other hand, will be almost entirely confined to areas where the water has a relatively high concentration of mineral ions, notably Ca^{2+}. (As mentioned, this correlation is less general in siliceous country with poor and much leached mineral soils.)

Calcareous soils will almost invariably be associated with highly calcareous minerotrophic water, which in some instances may even have reached the point of saturation with calcium bicarbonate. This calcium-saturated water will lose carbon dioxide on contact with air and heat, and calcium carbonate will then be precipitated in the minerotrophic peatland. The formation of calcareous deposits is very frequent in the highly calcareous Hawley Lake – Sutton Ridge area (Sjörs, 1961*b*) but was not found on Attawapiskat River, except locally on clayey (not peaty) wet river banks (p. 106) where moisture contained in the moss carpets is subject to strong evaporation in summer after the recess of the spring flood. Nevertheless, very large areas of minerotrophic peatland are obviously rather strongly calcareous also in the Attawapiskat River district, even if visible deposits of lime were not found.

Chemical Composition of Water

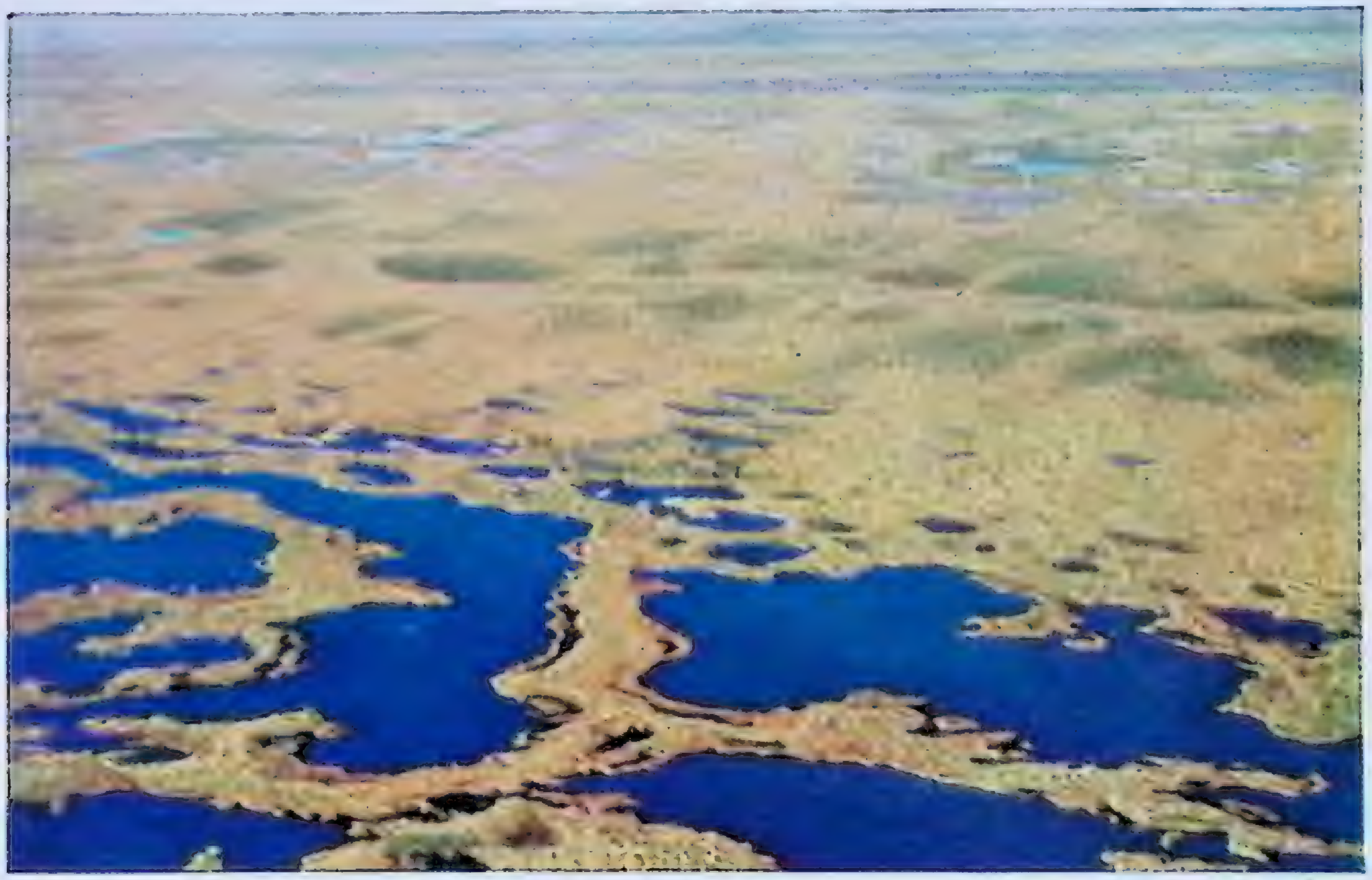
Chemical analysis of peat should preferably be made on fresh samples (Sjörs, 1961*a*), but considerable time and laboratory equipment are required. Because of this, we did not try to include peat analysis in the investigation, but three samples of water from peatland were taken for later analysis.

The water analyses are presented in Table 1. Number 1 is from an ombrotrophic bog-pool, No. 2 from a poor fen seepage with only few minerotrophic indicators, No. 3 from a strongly minerotrophic site (rich fen). Sample No. 4 was taken from Attawapiskat River (outside the reach of the Muketei River water, which is more humus-coloured and less turbid by suspended clay, but nearly equally alkaline; *see* Table 5, p. 98). The very low concentration of calcium ions in the bog-pool is typical of ombrotrophic conditions. The calcium ion concentration in the seepage is higher, and probably on the minerotrophic level (Witting, 1947, 1948, 1949). The ranges meet, and overlap to some extent, at about one milligram of calcium per litre. The low values for Mg^{2+}, Na^{+}, and Cl^{-} are typical of inland bogs. Also $SO_4{}^{2-}$ is low, as the site is far from the sea and not subject to air pollution. The river water is extremely low in Na^{+}, Cl^{-}, and $SO_4{}^{2-}$, and high only in Ca^{2+} and $HCO_3{}^{-}$. Being partly derived from the Precambrian area and from non-calcareous peatland, it is not extremely calcareous, and only half as calcareous as the Hawley Lake water (32 mg Ca per litre; Sjörs, 1961*b*). Still higher values are not uncommon in other northern calcareous areas: up to 74 mg per litre in calcareous lakes in Dalarna, Sweden (Lohammar, 1938); 25 to 108 in calcareous fens and springs in Jämtland, Sweden, and 40 to 58 in calcareous fens and up to 33 in lakes, in Swedish Lappland (Witting, 1949).

In addition, a number of pH determinations were carried out for water from peatland. Although probably too few to show the total ranges, they give good indication of the acidity in different types of peatland. The pH found in bog-hollows (Table 2, p. 70) is 4.0 to 4.6 and in bog-pools (ombrotrophic or nearly so) 4.5 to 5.1. These values are comparatively high for inland ombrotrophic bogs. In seepages (vegetation: poor fen) pH is 4.8 to 5.7 and in atypical bog-pools that probably receive minerotrophic water from below, 4.8 to 6.6 (Table 3, p. 80). Poor fens, other than the seepages, show pH 4.1 to 5.4, and rich fens 5.8 to 7.4 (Table 4, p. 96). Finally, wet patches on the river banks, springs, brooks, rivers, and the only lake visited (near Muketei River) usually proved slightly alkaline (Table 5, p. 98).

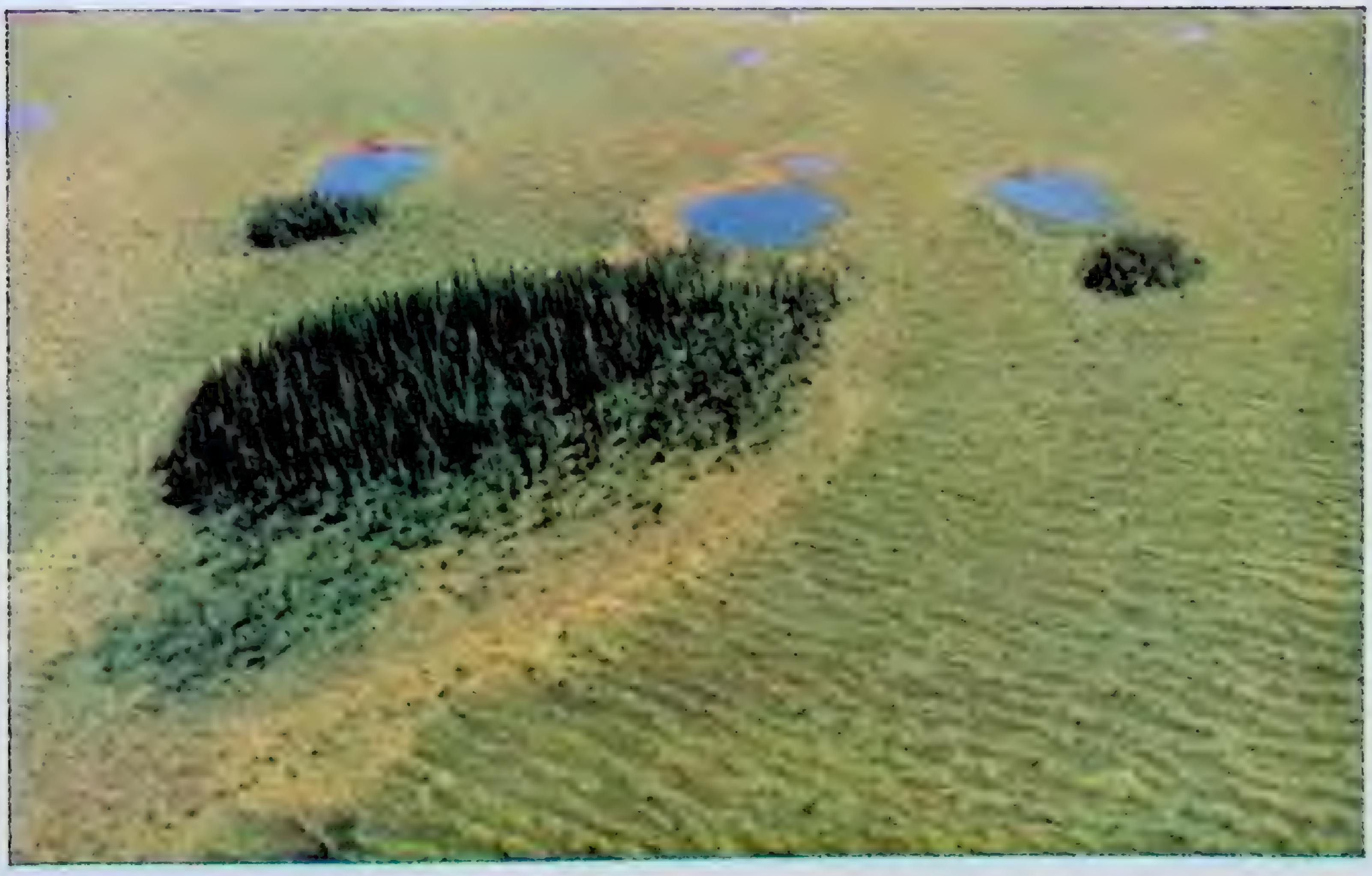
Minerotrophy in Very Extensive or Continuous Peatland

In a landscape where the peatland is discontinuous, mineral soil is exposed between the peat areas. In such landscapes, the minerotrophic peatland receives water from the areas covered by mineral soil, whereas the ombrotrophic peatland does not. One would expect, therefore, that any large area of continuous peatland would be entirely ombrotrophic, but this is not the case. There are some very extensive expanses of ombrotrophic peatland in Europe, notably in the west (e.g., the Easky bog in Ireland; Gorham & Sjörs, in prep.), but in many cases there occur "soaks" or strips with minerotrophic water even in the centre of large ombrotrophic bogs (Weber, 1902; Osvald, 1923). In northern and eastern Europe peat landscapes commonly include a high proportion of minerotrophic peatland even when the individual peat-covered areas are large and unbroken. This is the case for instance in Polesie (formerly Polish, now Russian). The Polesie peatlands were described by Kulczyński (1949), who also discussed



A. Part of the raised bog just northeast of the Attawapiskat-Muketei junction, of which a vertical view is shown as Plate VIII (p. 69) and a profile as Text Fig. 4 (p. 72). Note tapering "seepages" near middle of photo, sloping toward the brook that crosses the photo from left to right.

—*From* Arctic 12, *No. 1, 1959,* by permission



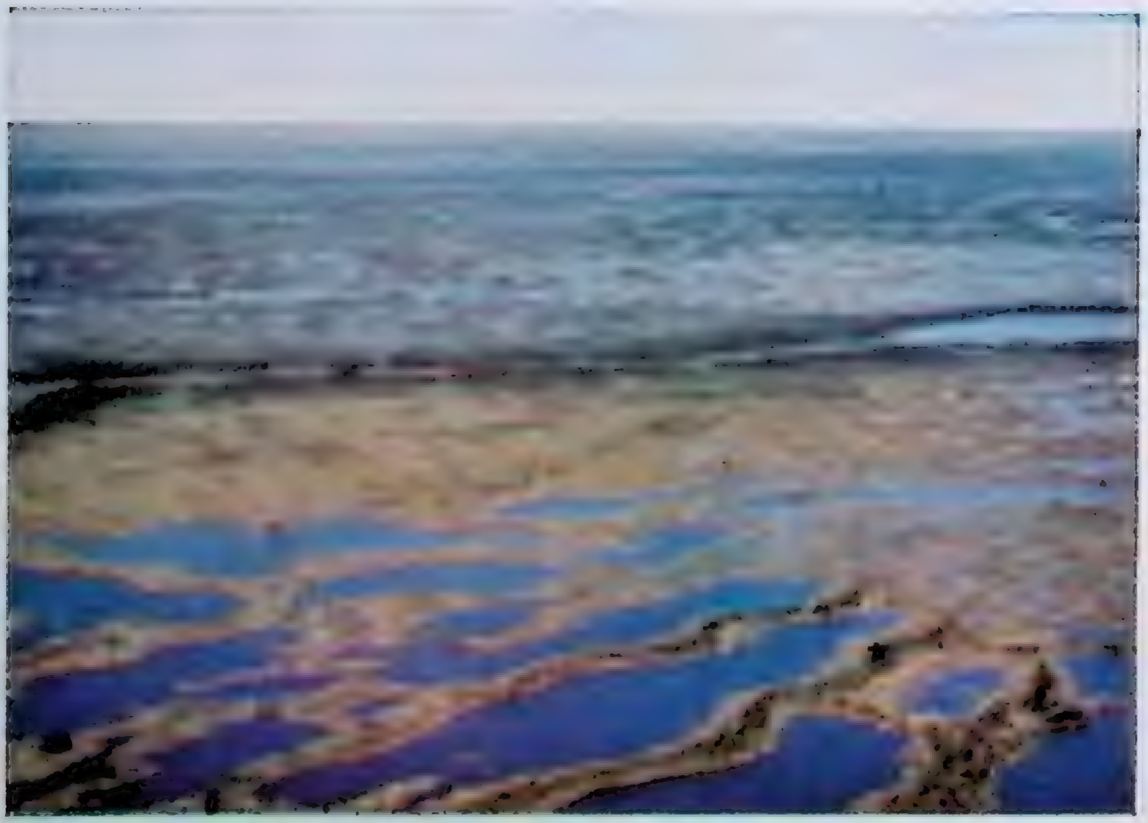
B. Black spruce islands in a minerotrophic fen that slopes toward the camera and shows a typical ridge-and-flark micro-pattern. Twelve miles southwest of the river junction (Plate VII, point c)

—*Photo A. E. Porsild. From* Arctic 12, *No. 1, 1959,* by permission

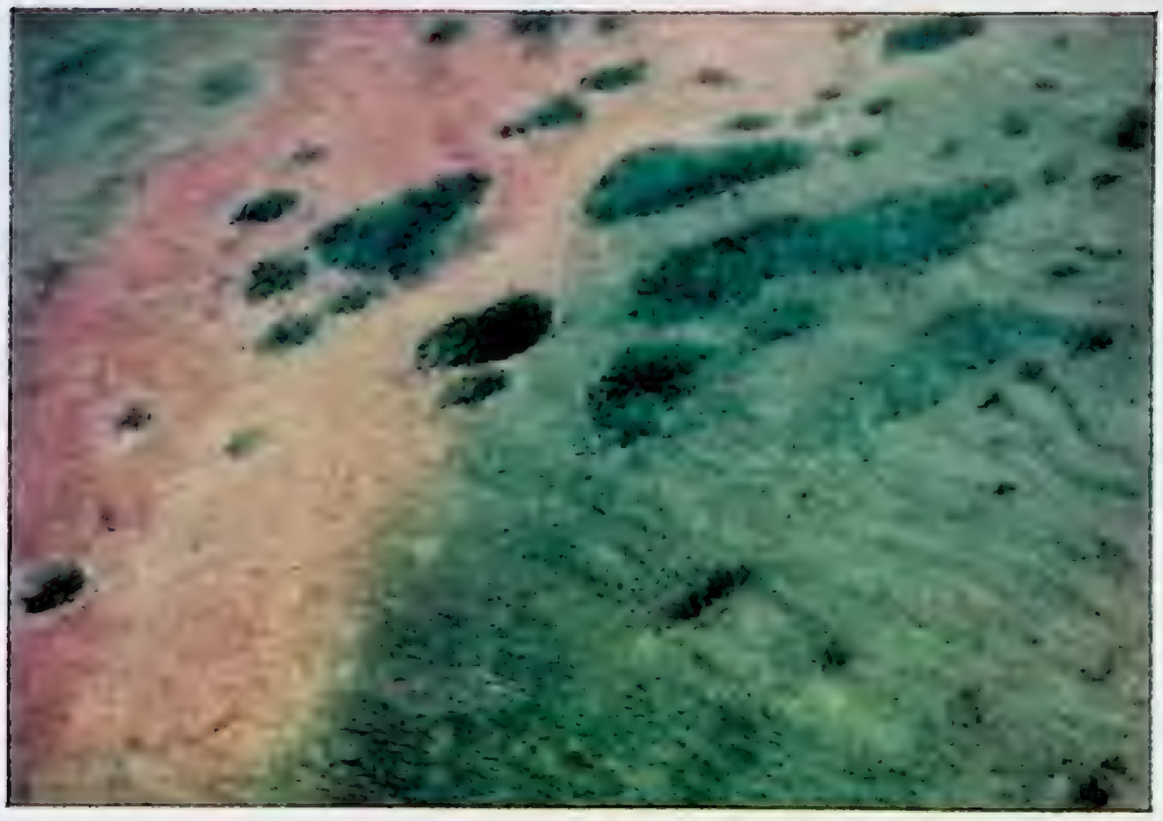
PLATE IV

A. Large expanse of minerotrophic fen; pattern barely visible. Small black spruce islands. Same area as in Plate VII (p. 66)

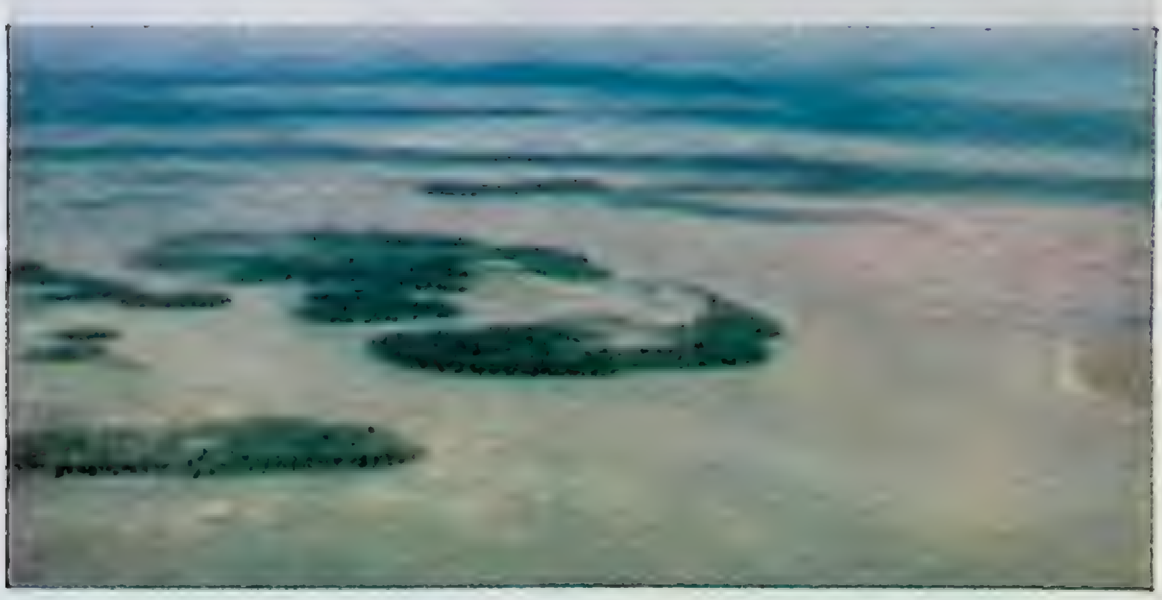
—Colour Plates IVA to VIB from ENDEAVOUR 20, No. 80, October 1961, by permission



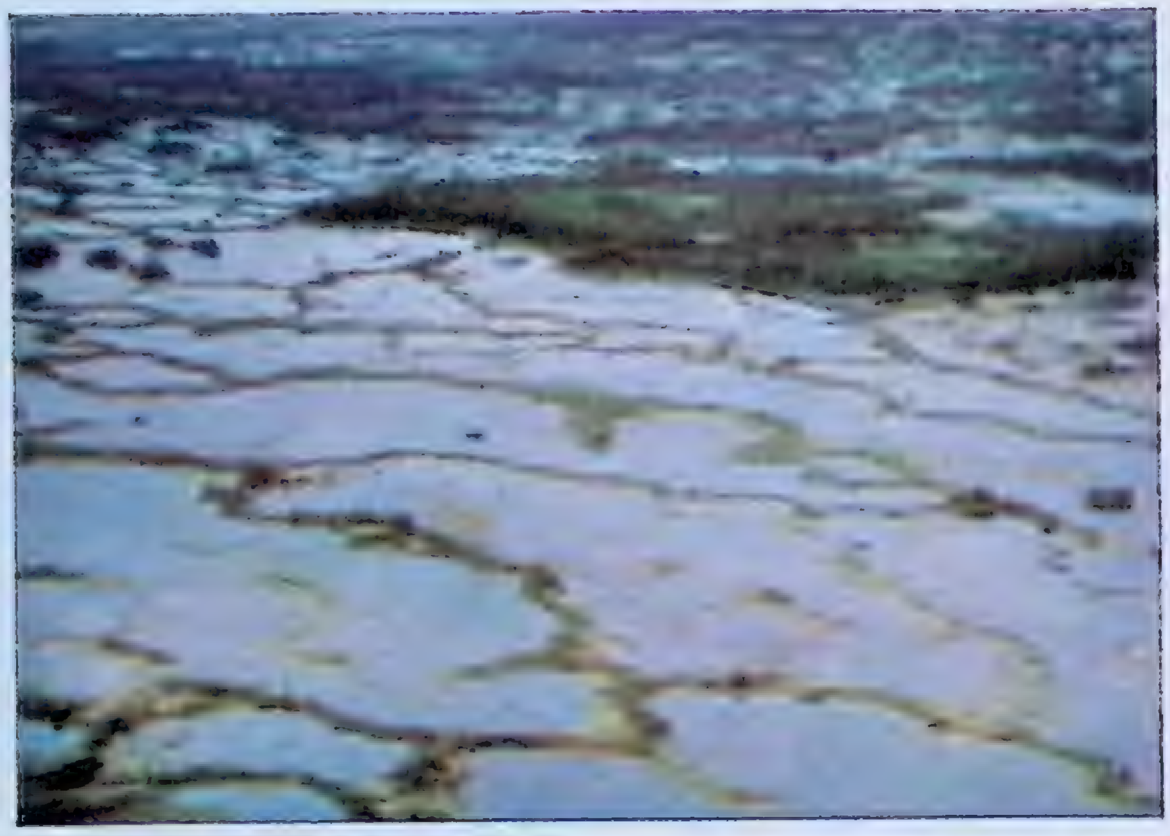
B. An ombrotrophic bog area immediately right of that shown on Colour Plate IIIA. The brook is expanded into a beaver pond (right). Black spruce on ridges between pools in foreground



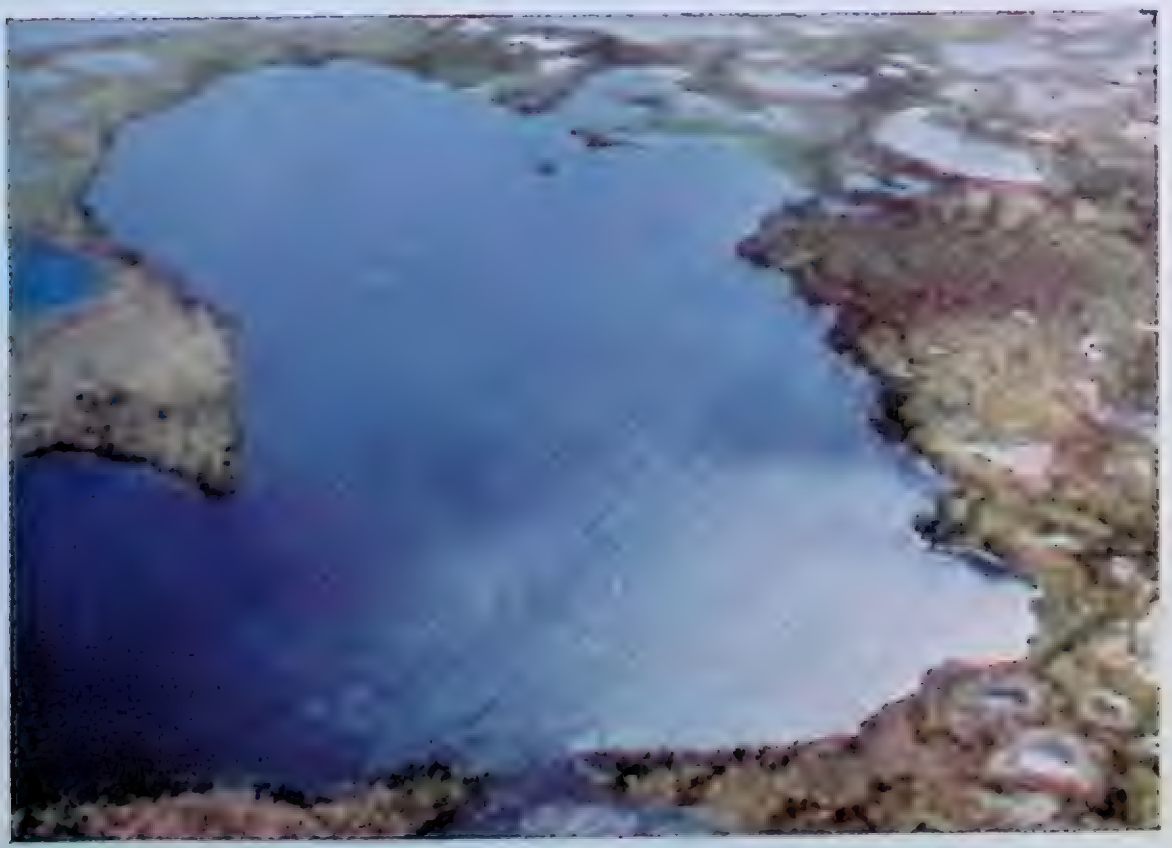
A. Large, circular, partly ring-shaped black spruce islands surrounded by minerotrophic peatland (fen) largely covered by low tamarack (*Larix laricina*). An ombrotrophic bog to the right. South of Matateto River



B. Left part ombrotrophic, colour probably mainly from *Sphagnum rubellum*; right part minerotrophic, with pattern at right angles to slope, green colour partly from small tamarack and dwarf birch. Black spruce islands in both parts. Near Kapiskau River



A. Extremely large flarks still covered by melt-water and separated by elevated ridges, partly with black spruce trees. Between Attawapiskat and Ekwan Rivers, about thirty miles from the coast. This type of pattern, reminiscent of terraced rice-fields, is not so common in the Hudson Bay lowland as in the Aapa areas of sub-arctic Lapland (Sweden and Finland) and (probably) the Labrador peninsula.



B. Lake probably formed from several coalescent lakes. To the right a bog being cut into by the lake. Sites rich in similar lakes are found in almost flat parts that constitute water divides between the catchment areas of large rivers. Near Kapiskau River the development of ombrotrophic and minerotrophic peat areas. In northern Sweden and Finland, even the most extensive peatlands are largely minerotrophic, with ombrotrophic areas usually restricted to certain peripheral parts.

In such extensive bodies of peat, all the minerotrophic influence can hardly be derived from the surrounding mineral soils, which may be several miles distant. Lundqvist (1951 *b*, p. 97) expressed strong doubt on this point, although he was certainly not right when stating that "all water is of ombrogenous type." A feature common to the minerotrophic peatland types under discussion is that they form very little peat at present, and therefore appreciable amounts of mineral nutrients are not taken out of circulation through any growth in thickness of the substrate (*see* further p. 90).

These problems have been mentioned here in order to show the inherent interest of extensive and uninterrupted peatland. For when minerotrophic areas occur in truly unbroken peatland, they could not be due to influence from exposed mineral soil. The peatland expanse needs to be very wide to exclude this possibility. The Hudson Bay lowland certainly meets the requirements for a study of uninterrupted peatland areas.

MAIN VEGETATION UNITS

The classification of peatland vegetation in the present paper makes use of the main units: the bog, the poor fen, and the rich fen, which were proposed by Du Rietz (e.g., 1942; 1949; 1950*a*, *b*, *c*; 1954*b*). They have been used also in the author's earlier works in Sweden, although in Sjörs, 1946, 1948, and (partly) 1950*a* and *b*, only the bog (or moss) type of vegetation, corresponding to ombrotrophic peatland, and the fen type, being minerotrophic, were treated as main units. The differentiation between poor fen and rich fen was then treated among other "directions of (vegetational) variation" (*see*, in particular, Sjörs, 1950*b* and 1952). These fen vegetation units were used as a first subdivision of the fens by Du Rietz and thus given priority to other possible ways of subdivision. They are related to acidity and other chemical variables in minerotrophic peat and water and are therefore important to distinguish in work where chemical conditions in fen are under discussion.

The vegetational characteristics of bog and of rich fen in the Hudson Bay lowland have been dealt with earlier (Sjörs, 1959; and in considerable detail, 1961*b*). They, as well as those of poor fen, will only be briefly summarized for the moment but will be more fully treated with regard to the Attawapiskat River area in the descriptive part of the paper.

Bog vegetation, in the restricted sense used here, is exclusively found in strictly ombrotrophic areas. It is very poor in species. In wooded parts, black spruce (*Picea mariana*) is dominant, and tamarack (*Larix laricina*) only subordinate. *Chamaedaphne calyculata*, *Ledum groenlandicum*, *Rubus chamaemorus*, *Kalmia polifolia*, *Andromeda polifolia*, *Eriophorum vaginatum* ssp. *spissum*, *Scirpus caespitosus* (*Trichophorum caespitosum*), *Scheuchzeria palustris*, *Carex limosa*, *Rhynchospora alba*, and *Sarracenia purpurea* are frequent vasculars in the Attawapiskat River area. The bryophytes are chiefly *Sphagna*, among which *Sphagnum fuscum* (brown), *S. rubellum* (red), *S. balticum* (yellowish), and *S. Lindbergii* (brown) should be mentioned because their colours dominate much of the bog surfaces when seen from the air. Light-coloured lichens occur on the hummocks.

The poor fen, which was not much discussed in the earlier reports, differs from the bog in the presence of a limited number of minerotrophic indicators. The poor fens in the Attawapiskat River area are nearly always adjacent to the ombrotrophic parts and are frequently dominated by the same species. Among the additional ones, *Menyanthes trifoliata, Juncus stygius* var. *Grayanus, Equisetum fluviatile, Eriophorum gracile,* and in wet pools *Utricularia vulgaris* and *U. intermedia* may be listed. A more marked difference is evident in the bryophyte flora.

The rich fen abounds in markedly minerotrophic and in many cases evidently basiphilous or calciphilous species, which will be more fully mentioned in the descriptions (p. 100). The drier parts, such as the ridges in the "ripplemarked" fens (p. 103), often carry scattered tamaracks *(Larix laricina)*, usually only a few feet high. This species is much more frequent in minerotrophic than in ombrotrophic sites. Its light green foliage gives the fens a special tinge that is easily observed from the air. A dense underscrub is usually present. Sedges and other cyperaceous species are prominent, as are a number of rich fen bryophytes. The latter are usually brownish in colour, varying from very dark in the wet depressions to bright golden yellow in the species of the drier parts (mainly *Campylium stellatum* and *Tomentypnum nitens*). The resulting colour impression in summer is one of dark olive green with a distinct tinge of light green from the tamaracks in the drier parts. Certain fen areas show a more grass-green colour, and fen mud-bottoms may be dark brown and not easily distinguished by colour from certain types of wet bog hollows.

The lines of demarcation between bog and fen are often sharply marked by colour contrast when seen from the air (Pl. VB, from Sjörs, 1961*c*). In such a case the contrast reflects an equally sharp boundary or limit of minerotrophic groundwater flow. Such a boundary of minerotrophy was termed "mineral soil water limit" (Thunmark, 1942), "exclusive fen plant limit" (Sjörs, 1946; Du Rietz, 1950*c*) or "boundary for mineral soil water indicators" (Du Rietz, 1954*b*). Further discussion and reference are found in the latter paper. Also Gorham (1952, 1957), Malmer and Sjörs (1955), and Malmer (1958, 1961) have discussed some ecological aspects on this type of vegetational and trophic boundary.

DISTRIBUTION AND STRUCTURE OF OMBROTROPHIC AND MINEROTROPHIC PEATLAND

From earlier descriptions and from air photographs it was evident that minerotrophic peatland areas are extensive in the Hudson Bay lowland. During our flights we could confirm that in most parts minerotrophic areas are predominant. The extent of ombrotrophic peatland was difficult to determine from the air, because it was not always possible to recognize the difference in colour and vegetation, particularly in the springtime condition in which we found the lowland during our first flight (June 20–23, 1957). The ombrotrophic type of drainage is usually determinable on black-and-white photographs even when made from a great height, but in an unfamiliar terrain the interpretation of peatland patterns may sometimes be faulty. Conventional aircraft are too fast for reliable and detailed reconnaissance, although observations can be made, and, when light conditions are favourable, colour photographs can be taken for subsequent study. Even from a low-flying helicopter, peatland reconnaissance requires rapid observation and interpretation. But unfortunately a helicopter was not available to us.

Well-marked patterns are common features of all peatland in the Hudson Bay area (Hustich, 1957*a* and *b*; Sjörs, 1959, 1961*c*), but these patterns are extremely variable. Rarely was it possible to correlate observed patterns with those described by Radforth (1952, 1953, 1955, 1956*a* and *b*, 1957, 1958) from areas with extensive permafrost in northeastern Manitoba. For rapid classification, Radforth has proposed a descriptive terminology: dermatoid, stipploid, terrazzoid, reticuloid, and marbloid (Radforth, 1956*a* and *b*) for patterns seen from high elevation; and from medium elevations: vermiculoid, planoid, intrusoid, cumuloid, apiculoid, and polygoid (Radforth, 1958). Excepting apiculoid, which in less technical language is spruce woodland, these terms do not tell us much about the patchwork of vegetation which, when seen from a distance, becomes a pattern. Nor can a pattern type in itself reveal the factors (types of drainage, trophic factors, corrosive oxidation, ice-expansion pressure, frost upheaval, etc.) that are at work, forming and arranging the elements of the pattern. Only when the pattern is first fully understood ecologically will it make sense (Sjörs, 1961*c*). Such understanding will not be possible without much experience from work on the ground (cf. Ritchie, e.g., 1960*c*; Ruuhijärvi, 1960; Allington, 1962), not necessarily in the same district as the aerial survey, but in any case in a region with similar physiographical and ecological conditions.

The direction of water flow is always easy to determine in patterned peatland, being at right angles to the ridges and depressions, which are thus parallel to the contour curves. This rule holds good in both ombrotrophic and minerotrophic peatland in all regions where patterns occur, except for cases where the pattern is influenced by strong winds or, possibly, where permafrost is prevalent. On a slope, even if it is very slight, both ridges and depressions are generally oblong or linear. The extension in the contour direction and the narrowness in the slope direction are very easily explained from the obvious fact that the water table, whether exposed or sub-surface, is exactly on the same level everywhere in each individual depression (Sjörs, 1946, 1948, 1961*c*).

Types of Ombrotrophic Peatland

In aerial view, ombrotrophic peatland is characterized by a drainage pattern that does not reveal any influx of water from outside. In flat country the drainage is more or less centrifugal or at least divergent, but it may also be bilateral or unilateral (cf. Text Fig. 5, p. 78). Ombrotrophic areas are frequently higher in level than adjacent minerotrophic peatland and may be up-domed (the typical raised bogs) although not always sloping toward all sides.

Several types of ombrotrophic areas occur in the Hudson Bay lowland. In the northern part of the subarctic woodland zone, and probably more frequently in the northwest, where permafrost is prevalent, there occur rather large, somewhat elevated areas of fairly dry peat, presumably permanently frozen and obviously ombrotrophic. They may correspond to peat plateaux (Radforth, 1955), or to certain elements of the "terrazoid" structure (Radforth, 1956*a* and *b*). In the subarctic zone, as in the Hawley Lake area (Sjörs, 1961*b*), one finds rounded ombrotrophic areas in which the peripheral parts are covered by black spruce and in the interior occupied by numerous largely lichen-covered, permanently frozen high hillocks (palsas) and scattered bog-pools, distributed among ordinary bog vegetation on peat which is not appreciably elevated and frozen only seasonally. The palsas are called "mounds" by Radforth (1955) and may (possibly and partly) be a feature of his "cumuloid" (1958) and "marbloid" (1956*a* and *b*) patterns (*see* further, Ritchie 1960*c*, where similar patterns have been successfully interpreted in terms of vegetation). Neither of these two types of ombrotrophic areas occurs in the inland as far south of Attawapiskat River. It must be left undecided to what extent ombrotrophic structures occur as hummocks, ridges, and elevated banks bordering pools and wet mud-bottom areas in "Smallpox Muskeg" and "Pothole Muskeg" (Hanson and Smith, 1950; Coombs, 1954).

On the middle Attawapiskat, ombrotrophic peatland is represented both by island-like structures and by bog areas usually of larger size. The former structures are elevated, sharply limited, and presumably permanently frozen, but, unlike the palsas, covered by very dense black spruce forest. These structures are mostly a few hundred metres across, and thus of larger extent than most palsas. They are termed "black spruce islands" (p. 107).

The remaining type of ombrotrophic peatland in the Attawapiskat River district is represented by bogs of different sizes, including both the miniature bogs mentioned previously and many medium-sized and even very large bogs. These ombrotrophic bogs are similar in outline to the palsa bogs mentioned above as typical of the more northern area near Hawley Lake, but they lack palsas. The large bogs are also in many respects similar to better-known raised bogs in the maritime parts of temperate East and West North America, in the East extending inland at least as far as Ottawa, where the Mer Bleue is a good example. Interesting examples of more northern types of ombrotrophic, raised bogs can be seen on aerial photographs from the Labrador-Quebec peninsula (Drummond, McKay, and Hare, 1952, Fig. 3; Hare and Taylor, 1956, Fig. 7, area B, Lake Melville lowland; Hamelin, 1957, Photo I, Côte Nord). Ombrotrophic sites probably occur also in central Ontario (*see*, e.g., Baldwin, 1958). We also observed ombrotrophic bogs on the Precambrian Shield north of Cochrane, but they appeared less strikingly developed, drier, more wooded, etc., and did not show the distinctly raised or convex topography which occurs both in some more maritime districts and in the flat Palaeozoic Hudson Bay lowland, where peatland formation is on such a large scale.

As particularly well stated by Kulczyński (1949) for Polesie, ombrotrophic peatland will develop on local watersheds, if the country is flat enough to permit formation of peat on them. This, according to the author's experience, holds good for Sweden too. Particularly favourable for ombrotrophic development are sites that are surrounded by either lakes or streams on two or more sides. In the latter case, large ombrotrophic bogs, sometimes even well domed, do occur far north of the general boundary drawn by Granlund (1932, p. 31) for Sweden (Sjörs, 1948). Northern types of ombrotrophic bogs were described from Finland by Ruuhijärvi (1960) and Eurola and Ruuhijärvi (1961).

In the middle Hudson Bay lowland we find the extremely flat major watersheds between the large river systems occupied by "Smallpox" and "Pothole" types of peatland (Hanson & Smith, 1950), which have an irregular type of drainage and very likely are only partly ombrotrophic (*see also* p. 92ff., where a complex of miniature bogs and minerotrophic passages is described). These and similar types cannot be discussed further without a survey on the ground, but it seems likely that effective isolation of an upper ombrotrophic peat and water stratum, above the subjacent minerotrophic peat and the mineral soil, cannot exist over very wide areas when the peat is shallow or is frequently perforated by pools and lakes. But there occur also numerous local watersheds of a secondary order, which will be particularly well developed in some areas with parallel streams. Such strikingly parallel rivers and brooks of all sizes are a characteristic feature of those parts of the Lowland where the general slope is distinct and regular. Between the parallel rivers and brooks, ridge-shaped, ombrotrophic bogs develop. They may be tens of miles long and usually one to a few miles wide, and they are clearly domed in cross-section.

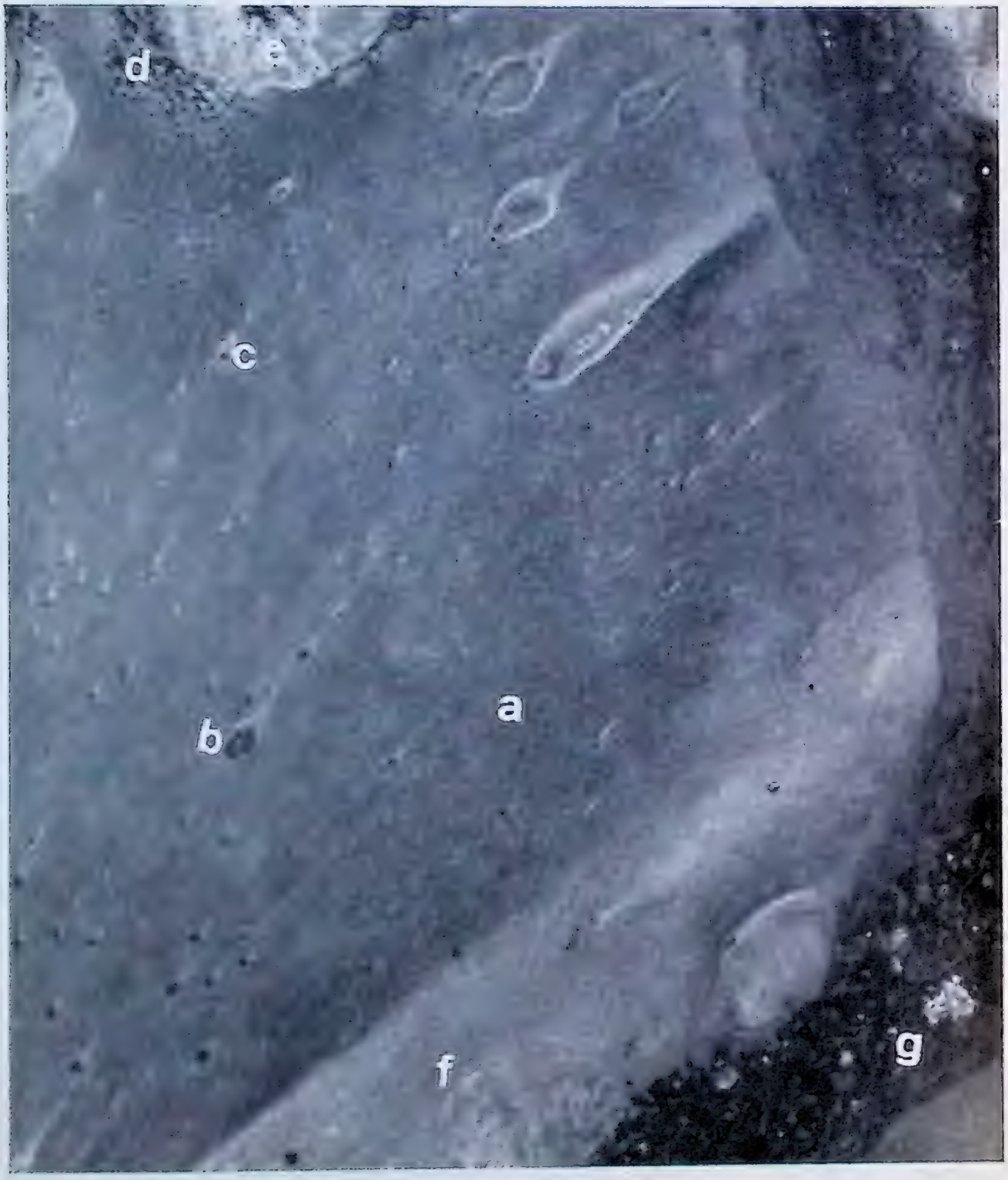
Such ombrotrophic bogs are particularly frequent on both sides of Muketei and Attawapiskat rivers, beginning about ten miles above their junction and continuing downstream along Attawapiskat River beyond its confluence with the south tributary, Missisa River. This area has a total length (W. to E.) of at least 30 to 40 miles and a width of about 7 to 15 miles. Ombrotrophic peatland covers more than half this area. To the north ombrotrophic areas are not so prevalent, even if a good example of a bog similar to the Attawapiskat River type was seen near Matateto River which is a tributary of Ekwan River. To the south and southwest, minerotrophic drainage is prevalent over very large areas.

The most striking feature in nearly all ombrotrophic areas, except the smallest ones, is the presence of numerous bog-pools, which largely replace normal bog hollows in the patterns of the bog expanses in this district. Also the drainage by "seepages" is peculiar to them (p. 99).

Types of Minerotrophic Peatland

The patterns of minerotrophic peatland generally show parallel or convergent directions of flow. Besides the mentioned difference in colour (p. 94), the densely "rippled" micropattern of much minerotrophic peatland (a compressed reticuloid pattern in Radforth's terms) is most characteristic in this district. The low ridges and the narrow depressions between them are at right angles to the slope. Similar, but frequently much wider, depressions in Fennoscandian minerotrophic peatland are termed "flarks" (Swedish) or "rimpis" (Finnish); *see*, e.g., the literature cited in Sjörs, 1946 (pp. 56–65), and in addition Sjörs, 1948 (pp. 139, 289, ff.).

PLATE VII



Vertical view of area *g*, Text Fig. 2 (p. 49), 12 miles S. W. of the river confluence. (*a*) Large, minerotrophic fen expanse sloping gently toward the northeast. (*b*) Black spruce islands, small and scattered. (*c*) The "island" shown on Colour Pl. IIIB. (*d*) Fen-pools. (*e*) Edge of an ombrotrophic bog. (*f*) Another bog (strictly ombrotrophic probably only in southern part). (*g*) Extensive area of elevated black spruce islands along a meandering small river. The treeless white patches may be either lichen-covered hillocks or carpets of some light-coloured *Sphagnum*.

—*Photo by R.C.A.F.*

1950*a* and *b*, 1961*c*; Lundqvist, 1951*b* (pp. 98–100), Ruuhijärvi, 1960 (pp. 74–90, 115–122, 209–220, etc.); Eurola & Ruuhijärvi, 1961; Allington, 1959 (pp. 72–80) and 1962. Occasional wide flarks and large fen pools also occur in the Attawapiskat River area.

Minerotrophic peatland is frequently fed by seepage from the ombrotrophic areas or from flat watersheds with miniature ombrotrophic bogs in a minerotrophic network. The flow of water (defined as the amount passing a cross-section of unit breadth per unit time) must, as a rule, be larger in minerotrophic areas. On the other hand, minerotrophic areas are drained by brooks and streams. In several cases it can be noted, on aerial photographs, that minerotrophic areas taper in their downstream part, ending as incipient streams.

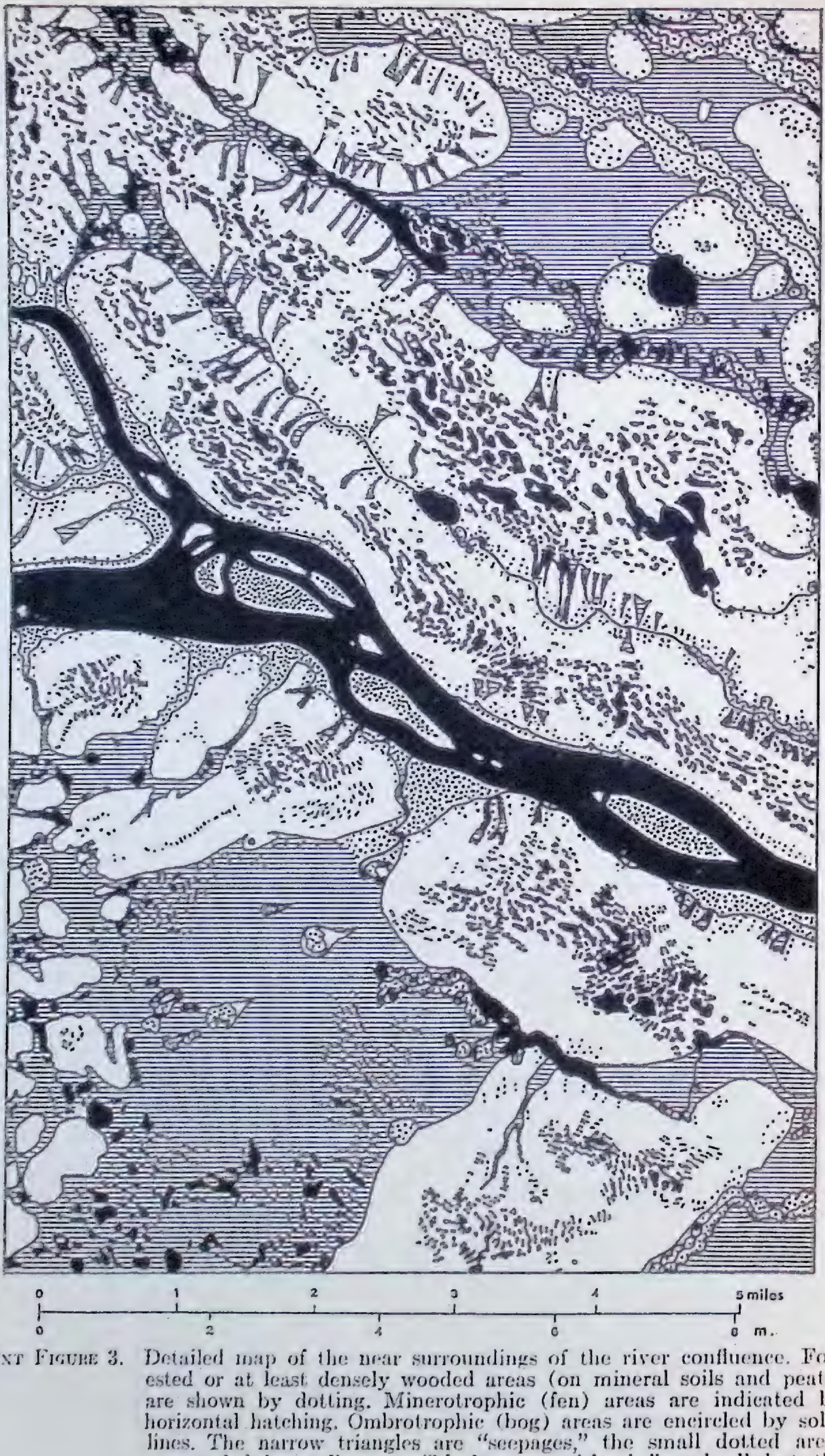
There are also some minerotrophic peatlands within reach of flood waters of brooks and rivers. Near brooks as well as in other sites the minerotrophic peatland may be well enough drained to be wooded by black spruce and tamarack of tree size. The minerotrophic wooded muskeg is much richer in species than the more abundantly occurring ombrotrophic type, including the two alders, dwarf birch, and even cedar (*Thuja occidentalis*), in addition to numerous minerotrophic sedges, other vascular plants, and bryophytes. On small streams and ponds, minerotrophic wet areas are occasionally widened by the beaver, resulting in drowning of trees by the damming. A different, very wet type of minerotrophic quaking fen occurs in certain abandoned river channels.

DESCRIPTION OF THE OMBROTROPHIC PEATLAND

Topography and Habitat Factors

Topography of Bogs

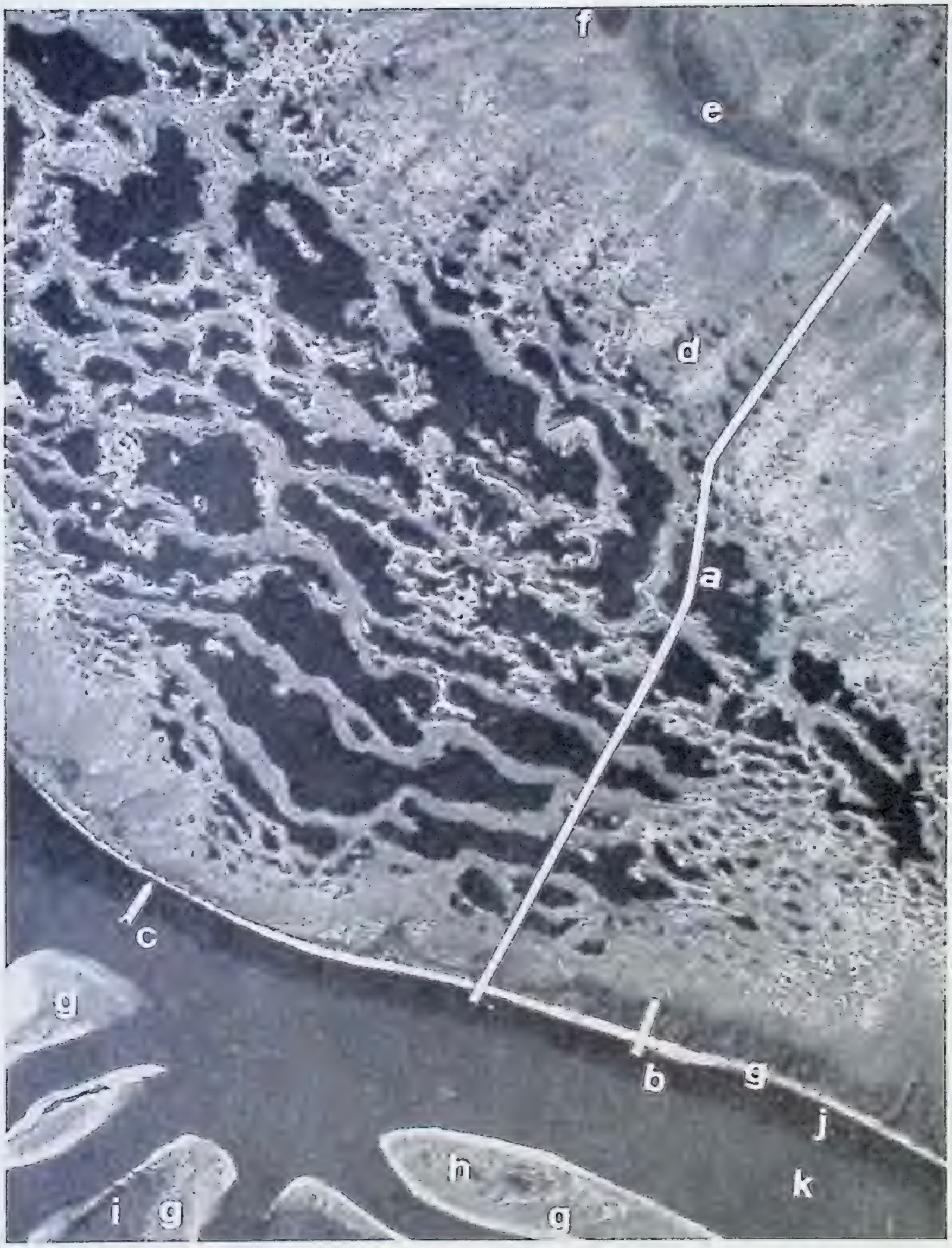
The ombrotrophic bogs show variants of a weakly domed or ridge-shaped topography. The large bogs along Attawapiskat River are regularly ridge-shaped. The convexity of their cross-section probably never exceeds ten feet, although it may appear to be more when the bog is seen from an eroded river bank. Other bogs, particularly in the Muketei part of the area, are irregular in outline but probably still more or less domed. The smaller bogs scattered through the mainly minerotrophic areas, for instance in the northeast corner of the area shown in Text Fig. 3, are often nearly circular, with diameters of about half a mile to one mile, i.e., about the same shape and size as many of the domed bogs in the Swedish lowlands (e.g.; Ryggmossen: *see* Du Rietz and Nannfeldt, 1925; Witting, 1948; Du Rietz, 1948, 1950*c*; Gorham, 1952). On the south side of the Attawapiskat we observed some bogs that slope unilaterally toward the river, but with somewhat divergent directions of slope, as seen from the fan-like arrangement of the hollows and bog-pools. These bogs are comparable in shape to some Swedish upland bogs (Osvald, 1930; Sjörs, 1948; Olausson, 1957) and also to the individual bogs of the Silver Flowe complex in S.W. Scotland (Ratcliffe and Walker, 1958). The occurrence of different topographic bog types in the same area shows that these types are more dependent on the relief of the underlying mineral ground, and less on the climate than has generally been believed (Granlund, 1932; Osvald, 1930, 1937, 1949, etc.)



TEXT FIGURE 3. Detailed map of the near surroundings of the river confluence. Forested or at least densely wooded areas (on mineral soils and peats) are shown by dotting. Minerotrophic (fen) areas are indicated by horizontal hatching. Ombrotrophic (bog) areas are encircled by solid lines. The narrow triangles are "seepages," the small dotted areas surrounded by a line are "black spruce islands," and all but the smallest pools are shown in black. The "flarks" are usually too narrow and crowded for small scale mapping.

—*From* ARCTIC *12, No. 1, 1959*

PLATE VIII



Vertical view of the Transect Bog at the river confluence, area *d*, Text Fig. 2 (p. 49). (*a*) Large bog-pool traversed by Transect I (*see* Text Fig. 4, p. 72, and, for southern part, Text Fig. 6, folder at p. 88). (*b*) Transect II (Text Fig. 7, p. 118). (*c*) Peat section studied by Terasmae (Plate XXIV and text, p. 115). (*d*) Seepage. (*e*) Brook, flowing through black spruce muskeg. (*f*) Black spruce island (elevated above preceding). (*g*) River fore-shore with willow scrub, showing up in darker grey than the eroded clay shores. (*h*) Balsam poplar wood with a few white spruce trees. (*i*) Closed white spruce forest, with occasional black spruce trees. (*j*) Humus-coloured but clear water from the Muketei. (*k*) Water of the Attawapiskat proper, turbid with clay. —*Photo by R.C.A.F.*

TABLE 2

Field determinations of pH (glass electrode) in water from ombrotrophic bog

HUMMOCKS		
"TRANSECT BOG":		
42.	Transect I (64 m): Bog margin wooded by *Picea mariana*, with *Ledum groenlandicum*, *Chiogenes hispidula*, *Kalmia angustifolia*, *Vaccinium myrtilloides*, *Pleurozium Schreberi*, etc. Water at 30 cm depth in a dug pit	4.2
33.	Transect I (126 m): *Chamaedaphne*, *Sphagnum fuscum*, *magellanicum*, etc., water from a dug small pit	4.6
HOLLOWS		
"TRANSECT BOG":		
40.	Transect I (91 m): *Scheuchzeria*, *Carex oligosperma*, *C. pauciflora*, *Sphagnum rubellum*, *balticum*, *Dusenii*, etc	4.4
39.	Transect I (93 m): the same vegetation	4.4
36.	Transect I (106 m): *Scheuchzeria*, *Sarracenia*, *Sphagnum Dusenii*, etc., in 8 cm of water	4.4
35.	Transect I (109 m): *Chamaedaphne*, *Scheuchzeria*, *Sarracenia*, *Carex pauciflora*, *Sphagnum balticum*, *rubellum*, etc	4.4
31.	Transect I (193 m): *Scirpus caespitosus*, *Chamaedaphne*, *Sarracenia*, *Sphagnum rubellum*, *papillosum*, etc	4.4
50.	Transect I (342 m): *Rhynchospora alba*, *Sphagnum Dusenii*, *Lindbergii*, etc	4.0
52.	Transect I (440 m): *Scheuchzeria*, *Sphagnum Lindbergii*, etc	4.0
21.	*Carex paupercula*, *C. limosa*, *Sphagnum Lindbergii*, *Drepanocladus Schulzei*, etc.	4.0
27.	*Kalmia polifolia*, *Rhynchospora alba*, *Sphagnum Lindbergii*, etc	4.0
93.	*Scirpus caespitosus*, *Carex oligosperma*, *Sarracenia*, *Sphagnum balticum*, *rubellum*, *tenellum*, etc	4.1
ATTAWAPISKAT RIVER 2 MILES DOWNSTREAM, BOG ON S. SIDE:		
54.	*Scirpus caespitosus*, *Kalmia polifolia*, *Carex limosa*, *Sphagnum Dusenii*, *Lindbergii*, *papillosum*, etc	4.4
MUKETEI RIVER 7.5 MILES UPSTREAM, BOG ON S. SIDE:		
74.	*Scirpus caespitosus*, *Carex oligosperma*, *Sphagnum balticum*, *tenellum*, *Cladopodiella fluitans*	4.1
BOG-POOLS		
"TRANSECT BOG":		
32.	Pool 1: *Nuphar variegatum*; adjacent *Scheuchzeria*, *Eriophorum virginicum*, *Utricularia cornuta*, etc.	4.7
30.	Pool 2: *Nuphar variegatum*	4.5
87.	Water analysis No. 1 (Table 1), from the same pool	4.5
49.	Pool 3: large pool with fish	5.1
51.	Pool 4	4.6
53.	Pool 5	4.9
20.	0.5 m open water, adjacent *Scheuchzeria*, *Carex limosa*, *Sphagnum rubellum*	4.6
ATTAWAPISKAT RIVER 4.5 MILES UPSTREAM, BOG ON S. SIDE:		
64.	*Scheuchzeria*, *Drosera anglica* f. *pusilla*, *Sarracenia*, etc	4.8

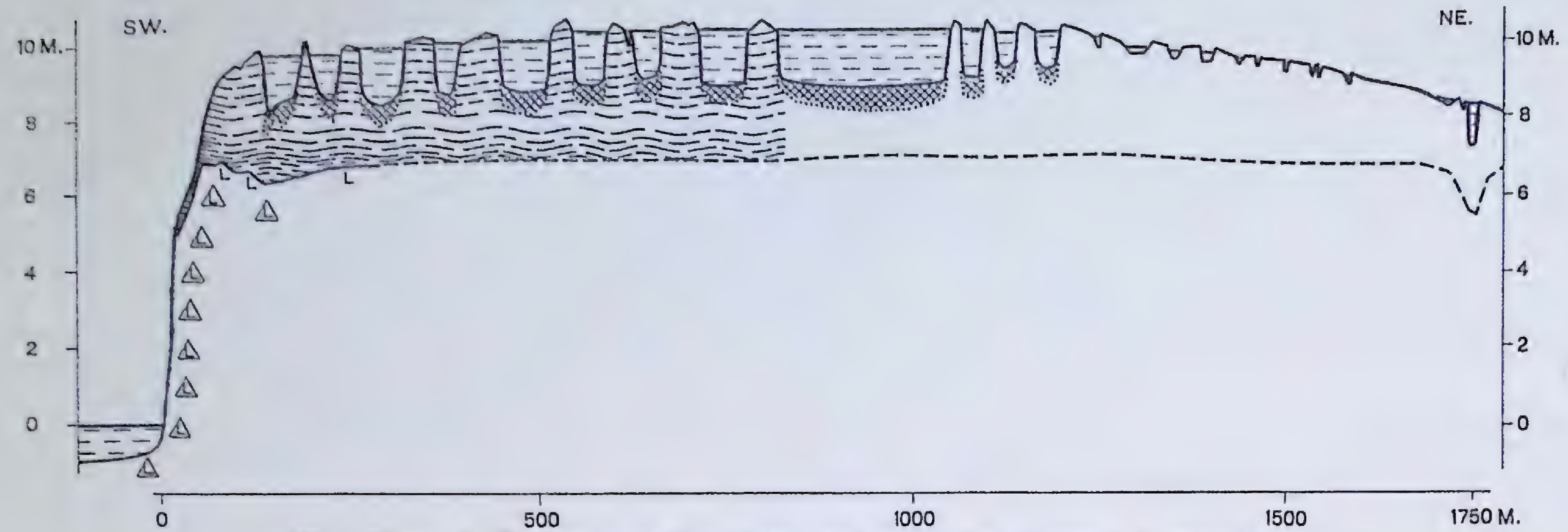
In cross-section the marginal parts of a convex bog slope considerably and are usually drier than the centre, which is only weakly domed. Except for wetter drainage strips (soaks, seepages), the marginal parts are wooded by low black spruce of varying density, with very little tamarack and with an undergrowth of low shrubs or dwarf-shrubs. Similar, but usually more scattered, woody cover occurs on the elevated hummocks and ridges in the central open bog expanse, between its hollows and pools.

Hollows and Bog-Pools

In small bog expanses and in narrow parts of the large expanses, the depressions on the bog surface are usually only of the type known as "hollows," i.e., the wet peat is covered by hydrophilous vegetation of cyperaceous plants, *Scheuchzeria* and *Sphagna,* or by algae on peaty mud; if the bog surface is submerged, the water is shallow and frequently dries up in dry seasons. In all large bogs in this district, there are, besides the hollows, also pools with open water. Values of pH in hollows and pools are given in Table 2. The pools are less acid than the hollows. The extent to which the expanses are occupied by bog-pools is variable, generally being greatest in the widest expanses, where the pools also reach their largest dimensions. In those investigated, the depth is about five feet, which is about half-way to the bottom of the peat deposit. In the more peripheral parts of the open bog expanses, where there is a distinct, although small slope, and in the unilaterally sloping bogs, the hollows and pools are elongated at right angles to the direction of the slope. The difference in level between consecutive hollows or pools on a sloping bog surface is only a few inches (3 to 26 cm, in Transect I, Text Figs. 4 and 6); the total gradient being of the magnitude 1:300 to 1:1000, or less, on the more central parts.

The bog Hammarmossen, which is the most extreme of the comparatively few Swedish bogs with a large number of bog-pools, is strikingly similar to many of the best developed bogs on the Attawapiskat River (Granlund, 1932, pp. 106–115; air photographs in Sjörs, 1948, p. 189 and Pl. 5, 1958, p. 89; notes on vegetation and water analyses in Witting, 1947, 1948). In Hammarmossen the bog-pools are about ten feet deep and reach nearly to the bottom of the bog, a condition which, however, is exceptional for Swedish bog-pools. Hammarmossen is ovate-concentric, not ridge-shaped, and has no "seepages."

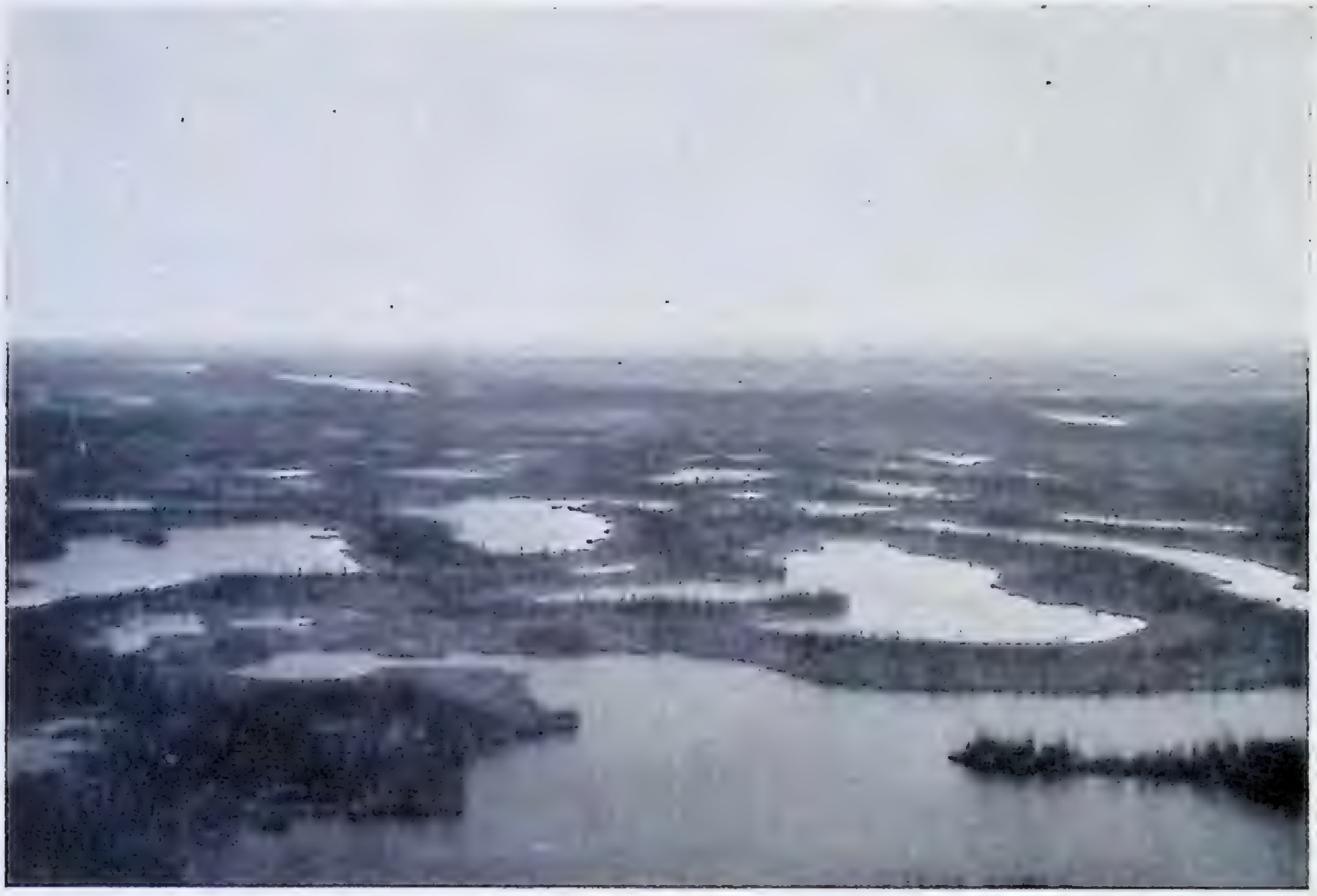
The bog-pools occupy similar positions as the ordinary bog-hollows, which occur beside them. Vegetation typical of hollows also surrounds certain bays of the pools, mostly near their ends. There is evidently a close relationship between hollows and pools. The bog-pools can be regarded as having developed from hollows in which peat formation has been retarded. As a consequence, the growth of the surrounding bog has caused the hollow surface to be submerged, and ultimately the hollow has changed into a basin of open water (Granlund, 1932, p. 114; Lundqvist, 1932, p. 79; 1933, p. 117; 1951*b*, pp. 128, 136; Ratcliffe & Walker, 1958). Lundqvist, who has made important contributions toward the understanding of the development of permanent flarks, hollows and pools (*see* particularly Lundqvist, 1951*b*), found that the formation of pools was usually preceded by a period when bog growth was checked temporarily, presumably by drought. Later, with



Text Figure 4. Profile across the ridge-shaped raised bog between Attawapiskat River and a beaver-dammed brook to the northeast. Part of the profile is shown enlarged as Text Fig. 6. In the remaining part (centre and right), the surface has been levelled, but the thickness of the peat was not measured. The right slope follows a seepage, the profile cutting several small flarks. L's indicate marine clay, L's in triangles, clayey glacial till. Vertical exaggeration 50:1.

—*From* Arctic *12, No. 1, 1959*

PLATE IX



Ombrotrophic area about 3.5 miles north-northwest of the river confluence. Black spruce forest on the fairly well-drained peat ridges between the large pools

—*Photo G. Sjörs*

an increasing balance of precipitation over evapo-transpiration, peat growth started anew on part of the bog surface, whereas places of incipient pool formation remained as water-saturated areas of muddy naked peat with scanty vegetation. After a few centuries they were drowned and ceased entirely to form peat. The present bottoms of the pools are covered by a thin layer of coarse detritus mud. This layer is about 40 cm deep in the pools of our transect.

The Attawapiskat bog-pools seem to belong in the same category as the Swedish examples, but further study is needed to determine their history and age. Some small and shallow pools, and parts of the large ones, may be younger than the rest. Wet, naked hollows that may represent initial stages of pools are seen frequently.

Corrosive Oxidation

Several ecological conditions, such as corrosive oxidation and ice uplift, are connected with the retardation of peat formation in wet hollows and pools. Peat formation is dependent on net photosynthesis less breakdown. The total photosynthesis is probably about the same in a hollow as on a hummock, but in a frequently water-saturated environment with few vascular plants and bryophytes, it will, to a great extent, be accomplished by algae. The film of algae is thin, but the production of oxygen in it will be very intense under favourable light conditions. The shallow water will reach gaseous equilibrium with the air. Particularly at low temperatures during night-time, this involves a high oxygen concentration. Thus, the presence of a thin layer of water above the peat surface, or a moist peat surface overgrown by algae, will both favour oxidizing conditions, although such conditions will be limited to the water and the thin superficial film covering the water-saturated substrate. One of the prerequisites for peat formation, however, is deficiency in oxygen below the water table. It is evident that the strongly oxidizing conditions in the superficial film will impede or retard peat formation (Sjörs, 1961*c*). Moreover, remains of macroplants (containing resistant substances, particularly lignin) are scarce, and the remains of the algae are more easily decayed.

The corrosion of peat surfaces by oxidation can easily be observed, not only on naked peat in wet bog-hollows, but on all kinds of mud-bottoms, including those occurring in fens (flarks, p. 103), and also at contact surfaces between peat and water of lakes, brooks, or springs, rich in oxygen (Sjörs, 1948, p. 84). Much of the so-called erosion described from peatland is actually oxidation. When wave or stream motion is strong enough to cause real erosion, the latter will be largely augmented by oxidative corrosion of the resistant fibres on the eroded surfaces, as well as by oxidation of part of the disintegrated peaty material.

PLATE X

A typical bog-pool with two peat islets. Sparse growth of *Scheuchzeria palustris* at water's edge

—*Photo G. Sjörs*

In an extensive study of the development of flarks and similar mud-bottomed areas in numerous peatlands within the Swedish province of Dalarna, Lundqvist (1951*b*, pp. 98–100, 116–119, 147, 177–179, etc.) was able to show that almost no peat had been formed in these habitats during the last two thousand to three thousand years. The considerable amount of organic matter produced in the flarks and mud-bottom bog-hollows during so long a period (including all the pollen that had blown into them) had disappeared almost without a trace; this is a definite proof of efficient corrosion, presumably by micro-biologically induced oxidation.

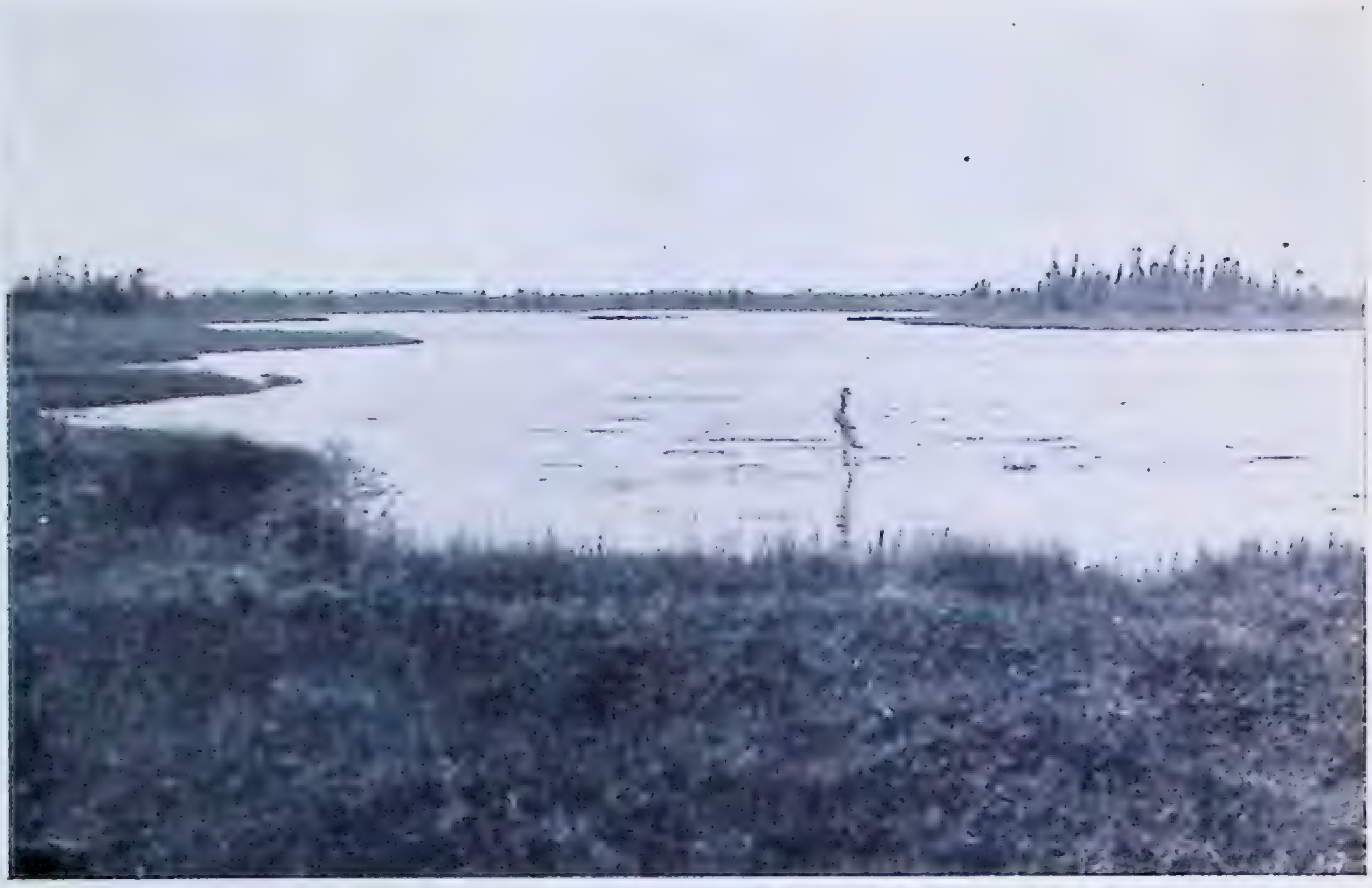
These conditions occur only when macro-vegetation is absent or scattered, and when, therefore, not only water supply but also light and nutrient conditions are better for algal growth than is the case in ordinary peatland (cf. Sjörs, 1946, p. 61). We find such conditions more prevalent in the main boreal and subarctic zones than in climatically more favoured zones. Besides the general slowing-down of plant production at low temperature and short growth season, the higher solubility of oxygen in water at low temperature may play a role. The snow cover, as well as the abundant meltwater during spring, is also important.

The general rate of peat formation is slow in the northern parts of the main boreal zone. It decreases still more through the subarctic and subalpine zones and is usually very low in most of the arctic and alpine zones. Besides the oxidative corrosion in hollows and pools, other conditions contribute to the slowness of peat formation in the cool regions. The slower growth of peat-forming vegetation has been mentioned. Where frost-heaved hummocks occur, they dry out superficially because of the presence of long persistent interior frost. True peat erosion by water or wind occurs as well, particularly in exposed localities. These features are to some extent influenced by other characteristics of regional climate rather than by temperature itself; e.g., maritime conditions and excess of precipitation over evapo-transpiration (cf. O. Tamm, 1959), and also by seasonal soil frost, permafrost, and solifluction, but these influences cannot be discussed here.

Uplift of Ice

Ice conditions in hollows and shallow pools though quite interesting are very little investigated. The ice is known to melt earlier in the hollows than in the hummocks. In hollows the melting of the more superficial part of the ice may result in a tendency of the still frozen deeper strata of peat to rise because of their buoyancy. Such ice uplift, or ruptures caused by it, were in fact observed in a few of the hollows (in two bogs) and most likely made possible the occurrence there of some plants alien to the ombrotrophic vegetation (*Menyanthes trifoliata, Drepanocladus badius, Sphagnum riparium, S. platyphyllum, Odontoschisma elongatum* (cf. Sjörs, 1959, Fig. 9, and Persson and Sjörs, 1960). The presence of these plants, which otherwise occur in minerotrophic environments (Table 3, p. 80), suggests that the disturbance, although quite local, has continued for a considerable time. In one place we even observed a distinct upwelling of water as from a small spring. Most likely this was due to local disturbance of short duration, for there was no indication that the water-level of a small, near-by pool was rising. Similar but stronger "spouts" were observed by

PLATE XI



Large bog-pool (third in Transect I). Note sunken peat with a small black spruce still alive. *Scheuchzeria palustris* growing in soft carpets of *Sphagnum Lindbergii, S. Dusenii,* etc.; firmer peat of *Sphagnum rubellum* and *fuscum* overgrown with *Rubus chamaemorus, Andromeda polifolia, Kalmia polifolia,* and some low *Chamaedaphne calyculata.*

—Photo G. Sjörs

Radforth (1954, pp. 52–56) and regarded as the result of "vertical confined lift," a dome of frozen peat sinking back again, causing water to be ejected for a day or two.

Disturbance through ice uplift ought to be strongest in shallow pools. But during the very cold winters of our area, even pools a few feet deep may freeze to the bottom. In spring, after the surface-ice has thawed, ice-sheets or lenses in the bottom peat may become detached and cause local uplift. The uplifted peat will subside later (Plate XI), but as it will probably be exposed to wave erosion and oxidation, the process will tend to make the pools deeper. In the fully developed deep pools, ice uplift is no more at work.

Frost Rifts and Ice Expansion

Frost cracks of a different type, or rather their marks, also were observed. They consisted of long, straight, narrow rifts through the wet *Sphagnum* carpets, often with ruptured rhizomes and other parts of vascular plants, as if made with a thin, sharp knife. These cracks, which were seen only rarely, correspond to the well-known cracks or rifts in lake ice which are caused by the contraction of the ice during cold spells. When water enters such cracks, it freezes causing the ice-sheet to expand horizontally; this again effects a pressure against the shores. In a bog such pressure will be directed toward the hummock ridges between the hollows and pools and will tend to make the ridges higher (particularly in autumn and early winter before their interior is frozen solid), as has been shown by Auer (1920) for the elevated ridges of peatland in northern Finland.

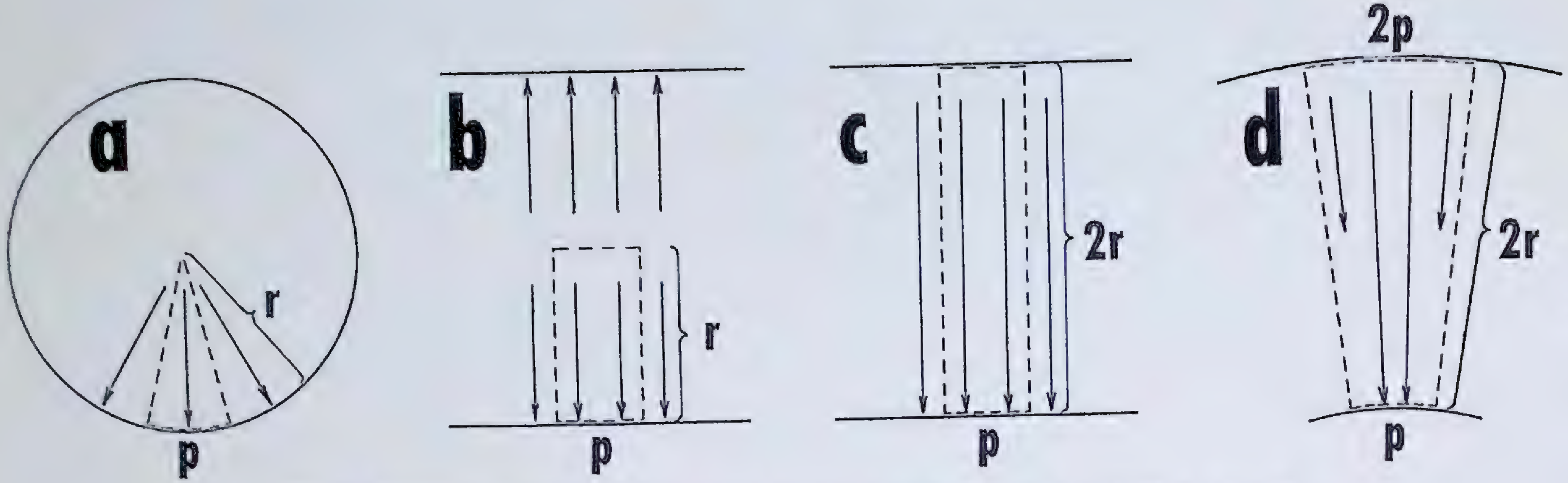
Seasonal Frost

Permafrost does not occur in open ombrotrophic bogs in the Attawapiskat River area. Seasonal frost persists very long in some hummocks. As late as July 25, 1957, we observed frozen peat inside the highest hummocks less than one foot below the surface, which was covered by light-coloured lichens. There is little doubt that this ice would melt entirely before the end of the summer. Because long-persistent ground ice may be misinterpreted as permafrost, it should be emphasized that owing to the general lag between soil and air temperature, the thawing process continues throughout August and September, when new ice may again be forming near the surface on cold nights.

Late-thawing seasonal ice may also be observed locally in bog margins covered by dense black spruce forest and on the steep eroded banks where river erosion has cut into peat. Such peat exposures are subject to deep frost penetration in winter. They probably lack the protection of a snow cover, so that cold air has access from the side as well as from above. In one south-facing exposure, solid ice remained in the peat on July 17, about one metre inside the vertical cliff and 40 cm below the upper surface, but undoubtedly disappeared later, for the deeper strata were not frozen.

Intensity of Run-Off Flow

There are no channels showing surface drainage on Attawapiskat bogs, but excess water may percolate slowly from pool to pool through the lowest parts of the ridges between them. Occasionally trails worn by muskrats may contribute to keeping adjacent pools on the same level, as was the case on the "summit" of the transect bog. The surplus of water is evidently not very large, for bogs have a high evaporation. They also possess a certain power of self-regulation, the wetness of the exposed surface of *Sphagnum* and other vegetation diminishing in dry periods and increasing in wet weather. After rains, evaporation from the bog surface is even likely to be greater than from a comparable lake surface, because the evaporating surface is greater and the loss of water is further augmented by the transpiration of the growing plants. Surfaces of several square miles of bog nevertheless produce a considerable run-off. On bogs with divergent slope directions, the run-off is spread, and its intensity diminished to a great extent. If a circular, concentrically domed bog (Text Fig. 5*a*) is compared with one sloping bilaterally (*b*) with the same transverse section as the diameter of the circular bog, the run-off per unit distance of periphery of the circular bog is half as large as the run-off traversing the same distance of side of the bilateral bog. In a unilaterally sloping bog



Text Figure 5. The run-off from (*a*) a circular domed bog, (*b*) a bilaterally sloping bog, (*c*) a unilaterally sloping bog, and (*d*) a crescent-shaped bog; all of them receiving no water from the environment. The run-off traversing the distance p is derived from the area surrounded by a broken line, which in (*a*) is $pr/2$, in (*b*) pr, in (*c*) $2pr$, and in (*d*) $3pr$.

(*c*), it is twice as large. In the rare cases of crescent-shaped ombrotrophic bogs (*d*), it will be still higher.[1]

Seepages

In the middle Attawapiskat area, a particular type of raised bog drainage occurs which has probably not been described from elsewhere, although the "Rüllen," described by Weber (1902) from the very large Augstumalmoor in East Prussia, represents a related type. At fairly regular intervals of a few hundred metres, we find so-called seepages (Sjörs, 1959, p. 11; a term suggested by Porsild), which run down the lateral slope, crossing the contours at right angles. Each seepage is slightly lowered in relation to the tongues of drier black spruce marginal bog between them and usually tapers gradually downslope, at the same time becoming more marked. It consists of a ladder-like row of small, shallow, narrow pools or "flarks" (*mares* in the French terminology used by Hamelin, 1957) in a step-like arrangement, the pools paralleling the contours and at right angles to the slope, as usual. Between the pools are drier, slightly damming embankments (*lanières,* op. cit.) but no high hummocks or ridges which would impede the drainage more strongly.

The moving water in the seepages, although derived from the ombrotrophic bog expanse, has higher pH values (Table 3) than the bog itself (Table 2, p. 70). On the bog, the large pools are not so acid as is usual in ombrotrophic bogs, and their waters are not so brown from dissolved humus colloids; the bottom is clearly visible at a depth of about 5 feet. Owing to the ice uplift phenomenon mentioned, presumably slightly minerotrophic water reaches the surface in certain pools. But nevertheless, the acidity in the run-off water of the seepages is very remarkably reduced if compared with that of the original bog water. Unfortunately we have only one chemical analysis from a seepage (Table 1, No. 2, p. 58), and this is not from the transect bog. It shows a higher mineral content, particularly for Ca^{2+}, than the sample of ombrotrophic bog-pool water, but it would be premature to declare it definitely minerotrophic. If so, one has to discover whether minerotrophy is brought about by ice uplift, or by the more general process of diffusion from the calcareous subsoil, particularly through the thinner peat of the extensive pool bottoms. Another possibility may be the following.

If in a seepage or other site the access of mineral salts from outside is greater than the loss with run-off water, a deposition will take place, normally as mineral ions fixed in the growing peat. In case little or no new peat is formed, it would be possible that such a deposition could result in augmenting the mineral content of the existing peat, particularly if run-off is much less than the total precipitation.

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[1] The crescent-shaped bog, which is situated near the Gizzard River, tributary of the Bell River in western Quebec, and shown in Hamelin 1957, Plates II and III (pp. 91, 103), has a well developed ridge-and-pool complex (lanières et mares) exactly in the part which, according to the present theory, should be the wettest. Details on the vegetation are not given, but it seems possible that this part of the peatland may be minerotrophic to some extent; whereas the drier parts seem to be above minerotrophic influence. A similar case, hydro-topographically, is Silmamossen in the middle Swedish upland (south part of province Dalarna), described by Lundqvist, 1933 (pp. 117, 120, 121) and Sjörs, 1948 (pp. 215-218 and plate 9 B). In Silmamossen, minerotrophic vegetation appears in the lower interior portion of the crescent; *see* map in Sjörs, 1948 (p. 216).

TABLE 3

Field determinations of pH (glass electrode) in water from presumably minerotrophic pools and "seepages" on the bogs

POOLS ON CENTRAL EXPANSES	
"TRANSECT BOG":	
22. *Menyanthes, Carex limosa, Utricularia intermedia; Sphagnum riparium* adjacent	5.8
23. *Menyanthes, Utricularia vulgaris, intermedia, cornuta, Drepanocladus badius, Odontoschisma elongatum; Cetraria Delisei*	6.2
24. *Eriophorum gracile, Scheuchzeria, Calliergon stramineum, Sphagnum parvifolium, Jensenii, platyphyllum, Drepanocladus procerus, badius, Scapania paludicola*	6.5
66. Pool 9: *Menyanthes, Sphagnum Jensenii, Calliergon stramineum, Drepanocladus procerus*	6.6
ATTAWAPISKAT RIVER 2 MILES DOWNSTREAM, BOG ON S. SIDE:	
55. *Menyanthes, Scheuchzeria, Andromeda*, etc.	4.8
SEEPAGES	
"TRANSECT BOG":	
67. Pool 11; *Utricularia intermedia, vulgaris, Potamogeton alpinus* ssp. *tenuifolius, Menyanthes*, etc.	5.7
68. Pool 12 (communicating with preceding): *Potamogeton alpinus* ssp. *tenuifolius, Sphagnum pulchrum, Drepanocladus procerus;* adjacent *Scirpus hudsonianus, Arethusa bulbosa*	5.7
69. Pool (flark) 13: *Menyanthes, Juncus stygius* v. *americanus, Scirpus hudsonianus, Utricularia intermedia, Sphagnum pulchrum, Drepanocladus procerus*	5.2
70. Flark-pool 14: *Menyanthes, Carex limosa, Scheuchzeria, Eriophorum gracile, russeolum, Utricularia intermedia, Sphagnum papillosum, Dusenii, pulchrum, Drepanocladus procerus, Tomentypnum nitens* v. *falcifolium*	5.0
71. Flark-pool 15: Similar to preceding	5.0
72. Flark-pool 16: *Menyanthes, Juncus stygius* v. *americanus, Eriophorum gracile, russeolum, Utricularia intermedia, Scirpus hudsonianus, Arethusa bulbosa, Sphagnum subsecundum, Jensenii, Drepanocladus procerus*	5.0
25. Flark-pool in next seepage to the east: *Menyanthes, Equisetum fluviatile, Carex limosa, Betula pumila* v. *glandulifera, Utricularia intermedia, Sphagnum pulchrum, apiculatum, Dusenii, Drepanocladus procerus, Tomentypnum nitens* v. *falcifolium, Scapania paludicola, Calliergon stramineum*, etc.	5.2
ATTAWAPISKAT RIVER 3 MILES DOWNSTREAM, BOG ON S. SIDE:	
86. Flark-pool: *Utricularia intermedia, minor, cornuta, Rhynchospora alba, Juncus stygius* v. *americanus, Eriophorum virginicum, Sphagnum Jensenii, apiculatum, Dicranum leioneuron*, etc.; water analysis no. 2 (Table 1)	4.8

The mobility of the water in the seepages may facilitate the saturation of the peat with metal ions and the nutrient uptake of the plants. Moving water, as compared with stagnant, has been shown to augment the growth and total uptake of certain nutrients in peatland plants (Malmer and Sjörs, 1955, pp. 61–64).

The seepages harbour several plants that are absent from normal ombrotrophic bog and indicate "fen" conditions, i.e., indicators of minerotro-

PLATE XII

Dense low thicket of black spruce with few stems reaching above protective winter snow level. Transect bog

—*Photo G. Sjörs*

phy. These fen plants occur regularly in the seepages, and true poor fen vegetation is found between and in the shallow pools or flarks. The seepage vegetation will be described under "poor fen."

On the side of the transect bog that faces the river, no regular seepages occur. Steeper slope and, in part, river erosion of the original bog margin, with improved drainage, seem to be the reason for their absence. However, there are lower parts in the marginal zone corresponding to seepages, and below the small escarpment (formed by river erosion at normal high-water) numerous small springs appear. Their water must come from the bog and has probably made its way between the peat and the top layer of the mineral soil, dissolving some calcium carbonate. Where it breaks through the bank, it is only moderately humus-coloured and about neutral (pH 6.1–7.6; Table 5, p. 98), because it has, on its way, lost the chemical properties of bog-water. It spreads over the clayey river bank and irrigates patches of vegetation growing on wet clay but referable to "rich fen" (p. 106).

The Ombrotrophic Flora

The following vascular species have been found in undoubtedly ombrotrophic bog sites near Attawapiskat and Muketei rivers. The remarks on frequency refer only to occurrence in ombrotrophic vegetation (Regarding "hummock" and "hollow" *see* pp. 88–9).

Picea mariana. Dominant in marginal woods and on some of the hummock ridges, particularly between pools. Its height varies from about 6 to 10 m in marginal forest and 4 to 7 m on ridges between pools, to low shrubs with intense layering, i.e., vegetative propagation, on the open bog expanses.

Larix laricina. Always subordinate; fairly frequent on ridges between pools, reaching about 5 m in height.

Andromeda polifolia. Present almost everywhere but dominant or subdominant only in hollows and particularly on edges of bog-pools. Not noted as pure by Dutilly, Lepage, and Duman (1954), who listed *A. glaucophylla* (a more southern species) and its hybrids with *A. polifolia*. Porsild did not observe *A. glaucophylla*, nor any specimens suggesting hybridization, in the Attawapiskat River area. *A. polifolia* is common near Hawley Lake to the north (Sjörs, 1961*b*) and was seen at Winisk. Hustich (unpub. rept.) reports *A. polifolia* from Fort Severn and *A. glaucophylla* from Big Trout Lake.

Carex limosa. Chiefly in hollows: frequently dominant or co-dominant.

C. oligosperma. Only in some of the wet hollows, but fairly frequent.

C. paupercula. Medium wet hollows; scattered.

C. pauciflora. Not too dry hummocks; scattered. In greater quantity in poor fen. Also found at Hawley Lake (Sjörs, 1961*b*); not noted by Dutilly, Lepage, and Duman (1954).

C. trisperma. Hummocks and wooded parts; rare in ombrotrophic sites.

Chamaedaphne calyculata. Dominant or co-dominant in the field layer particularly in wooded bog margins and on hummocks and ridges; frequent in moderately wet hollows, sometimes even in water by the edges of pools, etc. About two feet high or less.

Chiogenes (Gaultheria) hispidula. Wooded bog margins, frequent; hummocks, scattered.

Drosera anglica f. *pusilla.* Wet hollows; frequent.

D. rotundifolia. Hummocks and not too wet hollows; common.

Empetrum hermaphroditum (E. nigrum var. *h.).* Dry hummocks; not frequent (called *E. nigrum* by Dutilly, Lepage, and Duman, 1954; *see,* however, Löve and Löve, 1959).

Eriophorum russeolum f. *albidum.* Edges of pools and very wet hollows; not common.

E. vaginatum ssp. *spissum.* Moderately wet hollows and edges of pools; frequently forming tussocks when dominant.

E. virginicum. Only in some of the hollows but fairly frequent. First reported for the James Bay area by Lepage and Baldwin, 1959, p. 52.

Geocaulon lividum (Comandra l.). Wooded bog margins, frequent; hummocks, scattered.

Kalmia angustifolia. Wooded bog margin; rare. The finds constitute a northern extension of its known range.

K. polifolia. Present almost everywhere on the bogs but rarely dominant.

Ledum groenlandicum. Chief dominant or co-dominant in wooded bog margins; co- or sub-dominant with *Chamaedaphne* on hummocks and ridges; less tolerant of wet conditions than *Chamaedaphne.*

Nuphar variegatum. Bog-pools; rare and local.

Pinguicula villosa. Hummocks; probably rare, but easily overlooked because of its diminutive size. Also at Fort Severn (Hustich, unpub. rept.) and at Hawley Lake (Sjörs, 1961*b*).

Rhynchospora alba. Wet hollows and edges of bog-pools; frequent and locally abundant. Seen in several localities both in bog and fen. New to the Hudson Bay lowland (but reported east of James Bay by Dutilly, Lepage, and Duman, 1958); a considerable northward extension of the known eastern N. American range.

Rubus chamaemorus. Hummocks and wooded parts; common, occasionally dominant, but fruiting rather poorly.

Sarracenia purpurea. Not too wet hollows; frequent. A northward extension of the known eastern range. Hustich (unpub. rept.) reports it from Big Trout Lake to the West (not in the lowland).

PLATE XIII

Utricularia cornuta, with *Rhynchospora alba* and *Drosera anglica* f. *pusilla* (left). Mud-bottom near edge of bog-pool. Transect bog

—*Photo G. Sjörs*

Scheuchzeria palustris v. *americana.* Wet hollows and edges of bog-pools; frequently a dominant.

Scirpus caespitosus ssp. *austriacus* (*Trichophorum c.* ssp. *a.*). Hollows; frequently dominant.

Smilacina trifolia. Wooded bog margins, not too dry hummocks, etc.; irregularly distributed on ombrotrophic sites.

Utricularia cornuta. Mud-hollows and edges of bog-pools; fairly frequent and locally abundant. New to the Hudson Bay lowlands; a considerable northward extension of its known range (cf. Baldwin, 1958, p. 223), although reported east of James Bay by Dutilly, Lepage, and Duman, 1958.

Vaccinium microcarpum (*Oxycoccus m.*). Hummocks; common. Not reported by Dutilly, Lepage, and Duman, 1954. Also at Hawley Lake (Sjörs, 1961*b*), Winisk (our notes), Fort Severn (Hustich, unpub. rept.), and further west.

V. myrtilloides. Wooded parts, chiefly the bog margins; frequent and locally dominant.

V. oxycoccus (*Oxycoccus quadripetalus*). Usually on wetter sites than *V. microcarpum*; common.

V. uliginosum. Mostly on rather dry sites; not frequent in the bogs.

V. vitis-idaea v. *minus.* Wooded parts, chiefly the bog margins; frequent, occasionally dominant in black spruce stands on comparatively dry peat.

Comparison with N. Fennoscandia

A comparison may be interesting between the ombrotrophic vascular flora of the present area of investigation and that of the part of Fennoscandia comparable in climatic and regional respects, i.e., the "northern coniferous forest region." Both areas are essentially non-maritime in regard to the ombrotrophic conditions, despite moderate distance from the sea. The vegetation of the ombrotrophic bogs is composed of closely comparable plant communities in the two areas (Sjörs, 1959).

The following taxa are common to ombrotrophic sites in both areas, and similar, or at least not appreciably different, as to vegetative morphology as well as ecology:

Andromeda polifolia

Carex limosa. Less confined to very wet sites in the Hudson Bay lowland, *see also* Sjörs, 1961b.

C. pauciflora. Not frequent in ombrotrophic sites at Attawapiskat River; only occasionally ombrotrophic in northern Fennoscandia.

Chamaedaphne calyculata. Range distinctly eastern in Fennoscandia.

Drosera anglica. In both areas represented chiefly by the northern, more short-leaved f. *pusilla*.

D. rotundifolia

Empetrum hermaphroditum

Pinguicula villosa

Rhynchospora alba. Mainly a sub-oceanic species, in both areas reaching the northern limit of its range. In eastern N. America it ranges from Newfoundland to Lake Superior, with an isolated occurrence in N. Saskatchewan. Although a southern species in Fennoscandia, it reaches N. Finland, where it is, however, more or less restricted to minerotrophic peatland (Ruuhijärvi, 1960) or even prevailingly meso-eutrophic (Kotilainen, 1951).

Rubus chamaemorus

Scheuchzeria palustris. Represented at Attawapiskat River by the feebly distinct v. *americana*.

Scirpus caespitosus ssp. *austriacus*. The same ssp. in both areas.

Vaccinium microcarpum

V. oxycoccus

V. uliginosum. A variable species in both continents.

A few taxa have more or less closely related "vicariads" in the Fennoscandian ombrotrophic bogs. The distinction is not only morphological, for some difference in ecological behaviour exists as well:

ATTAWAPISKAT RIVER AREA:	N. FENNOSCANDIA:
Eriophorum vaginatum ssp. *spissum*. This N.E. American taxon passes gradually into *E. vaginatum* of N.W. America (Porsild, 1957, pp. 43, 168).	*E. vaginatum*. The European type is coarser, with very firm and tough basal parts, and occurs also in dry hummocks.
Ledum groenlandicum. In wooded and non-wooded hummock sites.	*L. palustre*. Chiefly in wooded sites.
Vaccinium vitis-idaea ssp. *minus*. A distinct taxon which reaches northeasternmost Europe from the east (Hultén, 1949, p. 397); small and rather weak in competition with larger shrubs.	*V. vitis-idaea*. Strong in competition, but confined to wooded, chiefly marginal parts of the bogs.

The following taxa are ombrotrophic on Attawapiskat River and have counterparts in Fennoscandia, but these are not known to occur in ombrotrophic sites there:

Eriophorum russeolum. Northeastern in Fennoscandia, ecology little known.

Carex paupercula. This is the N. American representative of *C. magellanica* (agg.). Its Fennoscandian vicariad is generally called *C. magellanica* or (if regarded as separate from the S. American taxon) *C. irrigua.* It is not normally a constituent of ombrotrophic bogs in Fennoscandia, where it occurs most commonly in acid minerotrophic sites (poor fens).

Nuphar variegatum. Found in bog-pools. These are not very strongly acid (Table 2), and there is little competition for nutrients in their bottom mud. However, the European counterpart, *N. luteum,* does not grow in waters so poor in nutrients.

The following taxa of ombrotrophic occurrence grow only in one of the two areas and have no close relatives in the other:

ATTAWAPISKAT RIVER AREA:

Eriophorum virginicum
Carex oligosperma
C. trisperma
Chiogenes hispidula
Geocaulon lividum
Kalmia angustifolia
K. polifolia
Larix laricina
Picea mariana
Sarracenia purpurea
Smilacina trifolia
Utricularia cornuta
Vaccinium myrtilloides

N. FENNOSCANDIA:

Betula nana. In N. America confined to Greenland and Baffin Island (Porsild, 1957, p. 176).

Calluna vulgaris. Found only in easternmost N. America, where it is doubtfully indigenous.

Empetrum nigrum s. str. According to Löve & Löve, 1959, absent from N. America (and in any case from Attawapiskat River).

Pinus silvestris

Vaccinium myrtillus (should not be regarded as vicarious for *V. myrtilloides* or related species).

Picea abies, Betula pubescens, and a few other species occur only occasionally in ombrotrophic sites.

The total number of vascular species is 34 in the ombrotrophic bogs of the Attawapiskat area and only 23 in the bogs of the much larger and more variable N. Fennoscandian area. The latter figure illustrates the well-known relative poverty of the North European flora. Not counting vicarious taxa, 15 vascular species are common to the bogs of the two areas. The percentage of common vascular species is 44 for Attawapiskat River and no less than 65 for Fennoscandia.

A good measure of the floristic affinity between two areas or two types of vegetation is the quotient of similarity (Sørensen, 1948), i.e., 100 number of species shared, divided by the mean of the numbers of species for the two areas of vegetation types. This figure would be 53, which is exceptionally high for a comparison between widely separated parts of two continents. It may possibly be equalled only in some poor fen communities.

The similarity in the cryptogamic bottom layer vegetation is much greater. For the bryophytes of the ombrotrophic bogs in the two areas the quotient of similarity would be about 90. The following 31 species have been found in undoubtedly ombrotrophic sites in the Attawapiskat and Muketei bogs (for details, *see* Persson and Sjörs, 1960):

HEPATICAE:

Cephaloziella elachista
Cladopodiella fluitans
Microlepidozia setacea
Mylia anomala
Ptilidium ciliare
Pt. pulcherrimum

SPHAGNA:

Sphagnum balticum
S. compactum
S. cuspidatum
S. Dusenii
S. fuscum
S. Lindbergii
S. nemoreum (capillaceum)
S. papillosum
S. parvifolium (angustifolium, recurvum p.p.)
S. robustum (Russowii)
S. rubellum
S. tenellum

MUSCI:

Aulacomnium palustre
Calliergon stramineum
Dicranum Bergeri
D. Drummondii
D. polysetum (undulatum)
Drepanocladus Schulzei (fluitans v. *falcatum)*
Hylocomium splendens
Hypnum plicatulum
Orthodicranum flagellare
Pleurozium Schreberi
Pohlia nutans
Polytrichum affine (st[illegible]um)
Ptilium crista-castren[illegible]

The only two bryophytes found in Attawapiskat [illegible]otrophic bogs that do not occur in Fennoscandia, viz., *Dicranum Drummondii* and *Hypnum plicatulum*, as well as the circumboreal *Ptilium crista-castrensis*, which is not found in ombrotrophic sites in Fennoscandia, are all confined to the wooded margins when growing in the Attawapiskat River bogs. *Sphagnum papillosum*, which grows in large hollows and along pools in the Attawapiskat bogs, is absent in purely ombrotrophic sites in northern Fennoscandia but occurs abundantly in the hollows of ombrotrophic bogs in S.W. Sweden as well as in West Europe. The other eleven ombrotrophic *Sphagna* grow in closely comparable habitats in both areas. A considerable number of small bryophytes, mainly hepatics, known from ombrotrophic bogs in N. Fennoscandia, remain yet to be discovered in the Attawapiskat River area; however, seven of them were found in the bogs near Hawley Lake where bog bryophytes were more thoroughly collected, and one (*Riccardia latifrons*) was found in a poor fen near Attawapiskat River. Not yet reported from the Hudson Bay lowland are *Pohlia sphagnicola* (recorded from northern Manitoba, Ritchie, 1956*b*), *Orthocaulis Binsteadii, Calypogeia Neesiana,* and *Cephalozia Loitlesbergeri,* and possibly one or two other small hepatics may be added. These species are inconspicuous. As the above-mentioned *Dicranum Drummondii, Hypnum plicatulum,* and *Ptilium crista-castrensis* are lacking in the open bogs, the bryophyte vegetation of the latter therefore appears identical in the two areas, with only one conspicuous exception, the occurrence of *Sphagnum papillosum* in the ombrotrophic bogs near Attawapiskat River.

The lichen flora and vegetation were not investigated; but by and large the same species seem to be dominant or common in the two areas.

THE OMBROTROPHIC PLANT COMMUNITIES

The vegetation of the Attawapiskat bogs, like that of boreal bogs in general, consists of "hummock" and "hollow" communities.

The standard term "hollow" refers to depressions of very variable extent, seasonally water-logged or at least with water standing near the surface. Much deeper depressions, with permanent open water, are called "pools" (p. 71). A pool may form the centre of a hollow or be only partly lined with vegetation characteristic of the hollows. Separating the hollows (and, if present, pools) there occur slightly elevated structures termed "hummocks," generally built up by high *Sphagnum* cushions and usually covered by dwarf shrubs; the *Sphagna* are partly replaced by other bryophytes or by lichens.

In northern bogs the "hummocks" rarely occur isolated. On the contrary they cover large areas and frequently coalesce to form a more or less continuous reticulate pattern. The hollows thus form separate quagmires, each one enclosed and dammed by the surrounding hummocks, which rise one or two feet above the essentially horizontal surface of the hollow. The [illegible] sinks and rises to some extent with the water (Sjörs, 1948; [illegible], 1949), so that the difference in height appears greater in dry [illegible] An extensive, more elevated hummock (frozen solid in its interior [illegible] most of the summer) is called "pounikko" in N. Finland (*see* [illegible], 1960, p. 220), whereas a several-foot-high mound with a bulky permafrost core is termed "palsa" (*see* further p. 107)

Vegetation of Wooded Bog

The hummock vegetation is somewhat different in the wooded parts (the bog margins and certain ridges between the bog-pools) when compared to the hummocks of the open, less wooded parts. Transitions occur between wooded and open parts, and intermediate types of vegetation may even cover extensive areas of bog.

The wooded parts have a fairly dense cover of black spruce and scattered tamarack. Among the field layer[1] plants, the common dwarf-shrub species *Vaccinium myrtilloides* and the less common *Kalmia angustifolia,* though confined to this type as far as ombrotrophic bog vegetation is concerned, occur occasionally in seepages. *Chiogenes hispidula* and *Carex trisperma* were frequently observed in wooded parts of the bogs and only very rarely in more open parts; neither is confined to bogs. Dominance in the field layer of wooded bog is usually shared by *Ledum groenlandicum* and *Chamaedaphne calyculata,* the latter usually predominant in less densely wooded parts; in the more marginal parts *Vaccinium myrtilloides* or *V. vitis-idaea* subsp. *minus* are also sometimes dominant. In the bottom layer of wooded bog vegetation, *Sphagnum* is often less abundant than are other mosses, such as *Pleurozium, Hylocomium,* and *Dicranum,* which also occur in other forested sites (however, *D. Bergeri* is a

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[1] Definition of some phytosociological terms:

Vegetation (on land) is usually composed of layers: tree layer, tall shrub layer, field layer (dwarf-shrubs, herbs, grasses, etc.), bottom layer (lichens and bryophytes growing on the ground), epiphytes, etc. Locally each well-developed layer has one dominant or several co-dominant species (also sub-dominants may be distinguished). Dominance, referring to quantity (weight, volume, or cover) in a given local area, should not be confused with frequency, which depends on number of individuals (or shoots) in a small area (in floristics, frequency refers to number of occurrences in a large area).

Plant communities (of the middle rank discussed here, i.e., associations and alliances in the European sense) are distinguished by their species composition. Comparing two related plant communities, some species may be differential or preferential. A differential species is present in one and absent (or at least very scarce) in the other of two plant communities. A preferential species occurs in both but has decidedly higher dominance or frequency within one of them.

PLATE XIV

Small hollow near wooded margin of bog. *Larix laricina* and *Picea mariana* grow in low scrub of *Chamaedaphne* and *Ledum;* in the hollow *Carex oligosperma* and floating *Sphagnum balticum* and *Dusenii.* Transect bog

—*Photo G. Sjörs*

sphagnophilous species). The occurrence of *Ptilium crista-castrensis* and *Hypnum plicatulum* under black spruce stands near the bog margin has been mentioned (p. 86). A large portion of Transect I (Text Fig. 6, p. 114, to the left) as well as the upper (right) part of Transect II (Text Fig. 7, p. 118) lies in wooded bog.

Vegetation of Hummocks in Open Bog

The hummocks of the open bog (cf. Transect I) are not entirely treeless. Black spruce and tamarack occur frequently as shrubs or dwarf trees. The black spruce frequently grows in small thickets about three feet high, which are under snow cover in winter. Vegetative propagation by means of rooting branches (layering) prevails, particularly in the black spruce. The principal field layer dominant in the hummock vegetation of open bog is *Chamaedaphne,* although *Ledum* is also present in great quantity as a co-dominant or sub-dominant. *Rubus chamaemorus* and a few other vascular plants occur as local dominants. The chief bottom layer dominant is *Sphagnum fuscum. Pleurozium, Dicranum Bergeri,* and *Cladonia* species (*rangiferina, alpestris,* and a member of the *silvatica* group) are local dominants. *Vaccinium microcarpum* and *Drosera rotundifolia* are most frequently found in this vegetation. The tiny *Pinguicula villosa* was found a few times in *Sphagnum fuscum* cushions. Some of the mentioned species also grow in the hollows, particularly *Chamaedaphne* and *Drosera rotundifolia*. In both habitats are also found *Andromeda polifolia, Kalmia polifolia, Vaccinium oxycoccus,* etc., and even *Carex limosa,* which is, however, preferential to hollows.

Vegetation of Hollows

The vegetation of hollows is distinguished from hummock vegetation by means of differential and preferential species, among which should be mentioned *Scirpus caespitosus* ssp. *austriacus, Eriophorum vaginatum* ssp. *spissum, E. virginicum, Sarracenia purpurea, Utricularia cornuta, Scheuchzeria palustris, Carex oligosperma, Rhynchospora alba, Drosera anglica* f. *pusilla* (all of them more or less strictly differential), and *Carex limosa* (preferential). On the other hand, *Picea mariana, Larix laricina, Ledum groenlandicum, Rubus chamaemorus, Vaccinium microcarpum,* etc., must be regarded as differential or strongly preferential to the hummock vegetation, being absent or rare in hollows. *Chamaedaphne* and *Drosera rotundifolia* are preferential to the hummocks in a much weaker degree.

Three vegetation units can be distinguished in the hollows and characterized as follows:

Some parts of the hollows are comparatively firm, caespitose or, in places, more turf- or lawn-like and usually not much water-logged. Here *Scirpus caespitosum* ssp. *austriacus* or *Eriophorum vaginatum* ssp. *spissum* are dominant, occasionally also *Chamaedaphne, Carex limosa, Andromeda,* or *Kalmia polifolia.* The *Sphagnum* carpet is more or less continuous, *S. rubellum* usually being dominant in higher and *S. balticum* in lower parts. The latter species may be replaced by *S. Lindbergii, S. magellanicum* (which also may grow with *S. rubellum*), *S. tenellum* (feebly peat-forming), and so forth.

The wetter and often quaking parts of the hollows are partly covered by soft carpets of *Sphagnum,* chiefly formed by *S. Lindbergii* and *S. Dusenii* but also by *S. balticum, S. magellanicum, S. papillosum,* etc. In these carpets *Scheuchzeria palustris* is ubiquitous and often dominant, followed in abundance by *Carex limosa. Sarracenia purpurea* is frequent in such wet carpets and not often seen elsewhere. *Scirpus caespitosum* and *Eriophorum vaginatum* ssp. *spissum* grow only as scattered tussocks. Most other species of the hollows occur only occasionally in the soft wet carpets.

The third type, the "mud-bottom" hollows, does not differ much from the preceding type in species composition but is strikingly dissimilar in appearance. The individuals or tufts of various species grow singly or scattered on the peat which is submerged in wet periods, and overgrown by algae. Among the vascular species, none reaches a high degree of cover, but relative dominance is shared by (or distributed among) such species as *Rhynchospora alba, Scheuchzeria, Carex oligosperma,* and *C. limosa.* Although common only locally, *Utricularia cornuta* may be quite spectacular here at flowering time. The metabolism and nutritional ecology of this remarkable carnivorous species are puzzling, its vegetative parts being astonishingly small in comparison with the showy inflorescence. Also *Rhynchospora alba,* which develops from a small winter-bud, is inconspicuous except when flowering; both barely attract one's notice in early July but appear in abundance two or three weeks later. One special type of mud-bottom hollow is dominated by large but well-spaced tussocks of *Eriophorum vaginatum* ssp. *spissum,* which here fruits abundantly. Less plentiful but fairly characteristic of mud-bottoms are *E. virginicum, E. russeolum,* and *Drosera anglica* f. *pusilla. Sphagna* are frequent but do not form carpets. *Sphagnum papillosum, S. tenellum, S. Lindbergii, S. balticum,* and *S. Dusenii* may be mentioned. *Drepanocladus Schulzei* (*D. fluitans* var. *falcatum,* see Persson and Sjörs, 1960, p. 260) frequently replaces the *Sphagna,* whereas the most ubiquitous bryophyte in mud-bottoms is the small hepatic *Cladopodiella fluitans.*

Corresponding differences were noted in the vegetation found between the palsas in the palsa bogs near Hawley Lake about 100 miles north of Attawapiskat River (Sjörs, 1961*b*), although the vascular flora there lacks such conspicuous southern elements as *Sarracenia, Utricularia cornuta, Rhynchospora alba,* etc.

The recognition of three units of "hollow" vegetation rests on a distinction first made by Nordhagen (1943, p. 451), who suggested a corresponding subdivision of the vegetation of more or less acid wet peatland (mainly minerotrophic) in subalpine-alpine Norway.

All five principal plant communities of the Attawapiskat bogs have North European counterparts which are similar with respect to bottom layer vegetation, in part also to field layers. Thus closely corresponding units were described from the bogs of the middle Swedish uplands by Sjörs (1948). If we could disregard the floristic difference, the physiognomic similarity of these bogs would be still more striking considering that the two areas are nearly 3,500 miles apart.

Vegetation of Bog-pools

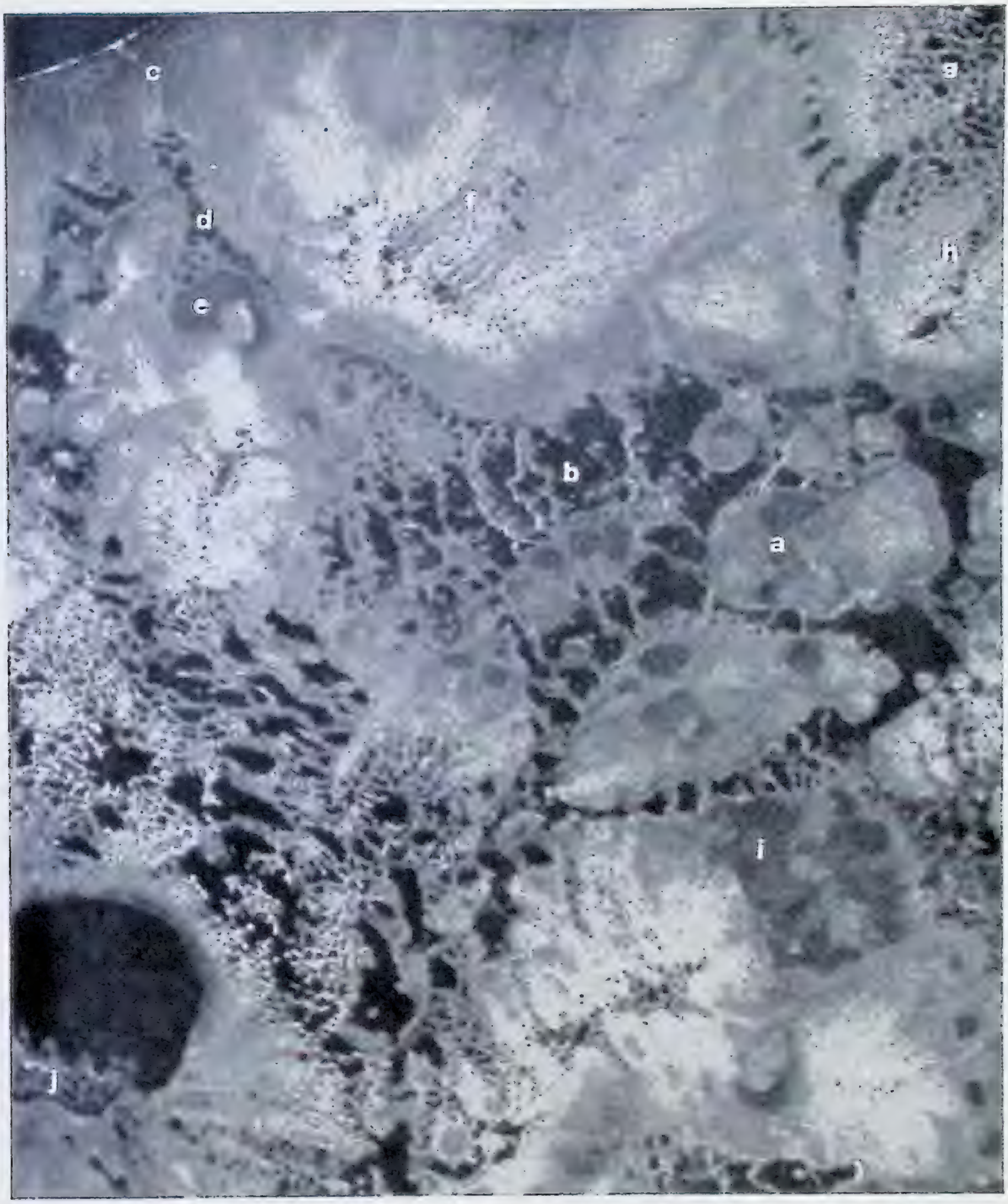
The bog-pools have a scanty vegetation. In shallow water *Scheuchzeria, Carex limosa,* and even *Andromeda* and *Chamaedaphne* may be seen growing on floating mats of *Sphagnum,* their roots extending into the peat along the shore. True aquatics are lacking except for very local *Nuphar variegatum.* There is some algal growth on the edges and bottom (not studied). Phytoplankton is scarce in contrast to zooplankton with abundant *Diaptomus* spp. (a new species reported by Reed, 1958). Various insect larvae, leeches, the leopard frog, and even small fishes were seen in bog-pools. Among the few birds seen was the Green-winged Teal (*Anas carolinensis* Gml.), and there were signs that some of the pools are frequented by muskrat.

DESCRIPTION OF THE MINEROTROPHIC PEATLAND

Topography and Habitat Factors

Origin of Minerotrophic Water

As mentioned earlier (p. 60–1), the extensive minerotrophic peatland areas in the Hudson Bay lowland differ from those in most other peatland districts in the general lack of direct access of water derived from exposed mineral soils. Despite this, some of the water in the peatlands acquires enough mineral ions to become distinctly minerotrophic.



Vertical view of area *c*, Text Fig. 2 (p. 49), south side of Attawapiskat River (top left corner). (*a*) Miniature bog. (*b*) Flark-pool, between narrow low "foot-bridge" ridges, all minerotrophic. (*c*) Wooded fen, with *Thuja occidentalis* occurrence (Table 7, p. 105). (*d*) Open rich fen, with series of shallow flarks (*see* Table 6, site B, p. 102). (*e*) Horseshoe-shaped black spruce island, also seen on Plate XXII A (p. 108)) and XXII B, (p. 108); the investigated one. (*f*) Ombrotrophic bog with small hollows and pools. (*g*) Bog with larger and very numerous pools, and also (*h*) seepages. (*i*) Black spruce patch, probably on permafrost, on ombrotrophic bog, an uncommon feature on bogs, but seen on several of the "miniature bogs." (*j*) Floating carpets of vegetation, rarely seen on the lakes

—*Photo by R.C.A.F.*

As mentioned, local minerotrophy occurs on the large, otherwise ombrotrophic bogs through frost cracks, ice uplift, contact with deeper strata in deep pools, and so forth (p. 75), and there is probably a tendency of the run-off water of the bogs to acquire a weak minerotrophy along the "seepages" (p. 79). As can be seen on air photographs, numerous such seepages are received by some of the minerotrophic peatland areas, but in other cases the seepages are caught by brooks and can only supply water locally along the latter.

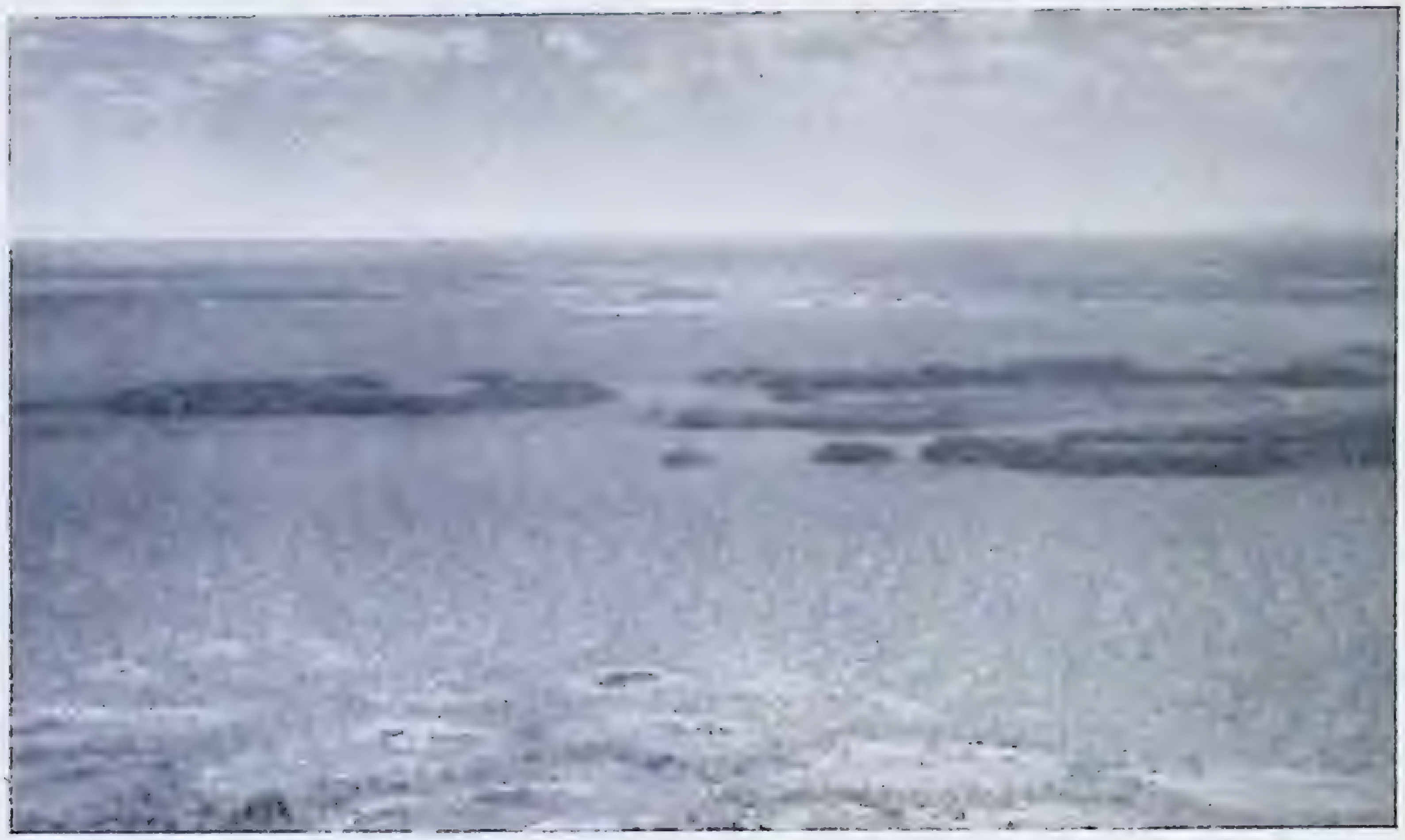
Some of the largest minerotrophic areas seem to receive most of their water from a peculiar complex type of peatland which covers large flat areas on the slightly higher ground between brooks. These areas (one of which is marked "*a*" and "*b*" in Plate XV) differ from the large ombrotrophic bogs in similar situations in being raised only partially. The raised parts form low miniature bogs of rounded, ellipsoid, or irregular outline, commonly up to a few hundred metres across, but sometimes larger, and doubtless ombrotrophic (*a* in Plate XV). Some are partly sparsely wooded, some nearly woodless and occupied by hummock vegetation. Small but dense black spruce stands occur occasionally within the bogs and are similar to the "black spruce islands" described later (p. 107). There are no hollows and bog-pools except in some of the larger of these miniature bogs.

Between the roundish miniature bogs there is a network of very wet lanes or passages (*b* in Plate XV) which collect the run-off from the miniature bogs, in addition to their own share of the precipitation. We were unable to reach typical areas, but a study of the pattern from the air as well as from aerial photographs indicates that the "passages" are minerotrophic. They frequently consist of a complex of broad but obviously shallow pools ("flarks") and very narrow, usually winding, low ridges ("ribs," "banks," "strings") separating the pools. Hamelin (1957) calls the pools or flarks "mares" and the ridges or strings "lanières." Narrow "passages" between close miniature bogs often consist of a single row of flarks, with the ridges appearing much as "footbridges" connecting the bogs. The ridges may be irregular and are frequently branched, but if there is a distinct slope, they are more or less parallel and at right angles to the slope.

Similar areas occur also without relation to miniature bogs. We visited one (*d* in Plate XV) situated above the "*Thuja* site" (*c*; see further p. 107) and below a horseshoe-shaped "black spruce island" (*e*; *see* further p. 107). The ridges in this case (*d*) were low and were covered by cyperaceous vegetation (not by bog hummock vegetation) and evidently were just as minerotrophic as the flarks between them.

Other ridges may be higher and seem to be partly overgrown by lichens on their highest parts (whitish on aerial photographs). Low trees (tamarack, locally also black spruce) occur on the latter. The aerial observations are not sufficient to give a more complete picture of the "string and broad flark" complexes.

We believe that peat formation is negligible in the flarks of these complexes. Therefore, they remain lower than the miniature bogs and have sufficient contact with the subjacent mineral soil for their water to remain minerotrophic or even calcareous.

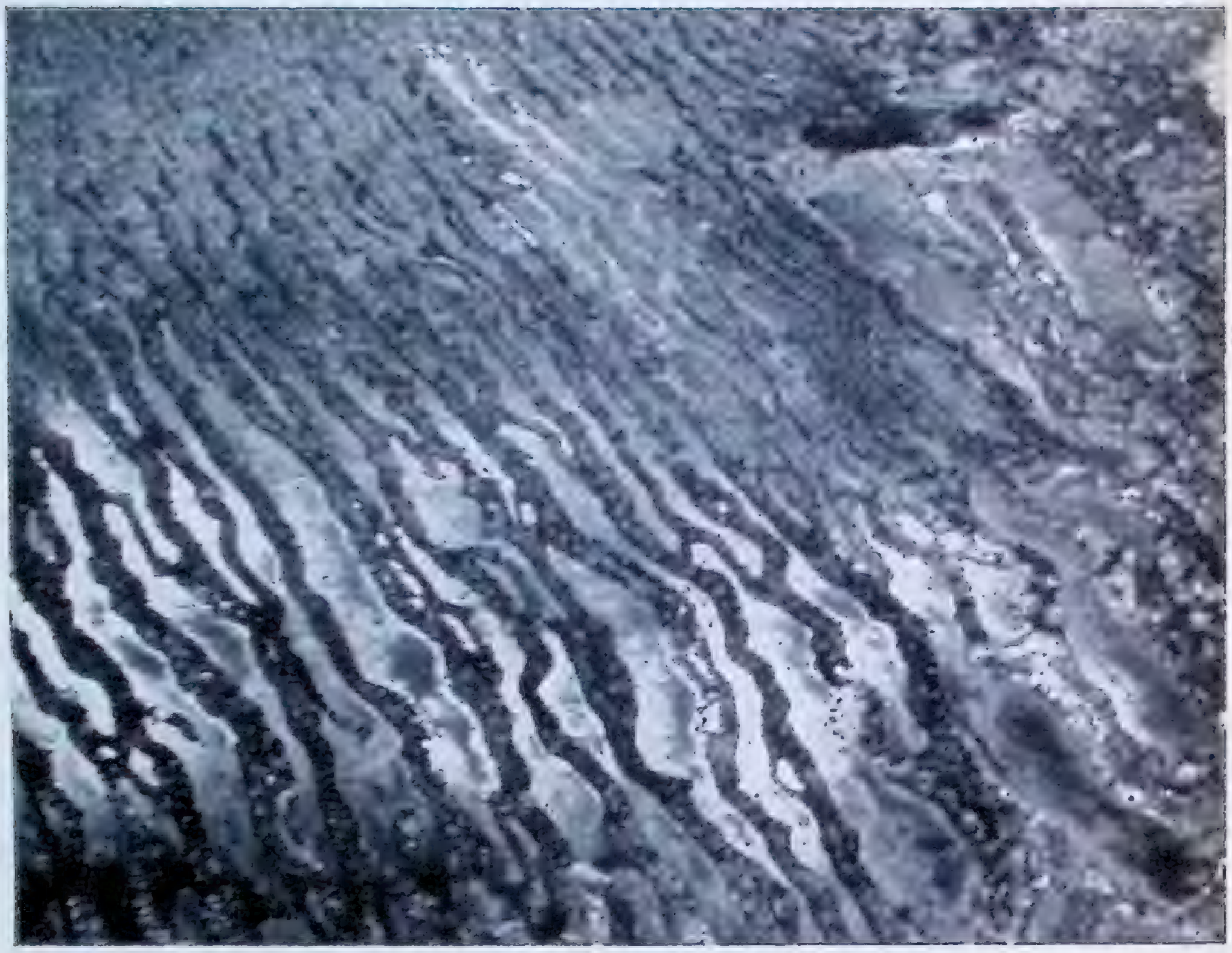


Northwest part of the large fen south of the river confluence, sloping gently toward the left. Foreground: circular shallow fen-pools separated by partly wooded ridges. Behind this: a "mottled" micropattern formed by comparatively dry flarks and low ridges covered by dwarf tamarack (*Larix laricina*). In centre: a few large, more or less annular black spruce islands

Minerotrophic Patterns: *Ridges, Flarks, and Fen-Pools*

If the run-off from such areas is not caught immediately by brooks or rivers, it will flow downslope on a broad front and may eventually irrigate very extensive areas. These constitute the enormous continuous expanses of minerotrophic peatland (fen) so characteristic of certain parts of the lowland. A prerequisite for their existence is the extraordinarily smooth topography with long, regular, and very slight slopes. The directions of water movement are nearly parallel in these large expanses. In smaller fens, they are often convergent in contrast to the frequently divergent water movements in ombrotrophic bogs. Most of the large fen expanses show a densely "rippled" micro-pattern with parallel, crowded low ridges and very narrow depressions (flarks) at right angles to the slope. The ridges and flarks are only a few metres wide but are endlessly repeated (*see* Plates XVI and XVII; also Hustich, 1957*b*, Figs. 7 and 14; Sjörs, 1959, Figs. 2 and 10, and 1961*c*, Fig. 3). There are often about 200 flarks to the mile, counted in the slope direction. From the general slope of 4 feet to the mile, the difference in level between consecutive flarks could be estimated at about one-quarter inch, i.e., less than one centimetre, but it is possible that the slope in the ripple-marked minerotrophic peatland is somewhat greater than the estimated general figure. The ridges rise about one foot or slightly more above the depressions, which are very shallow but are filled with water, at least during spring and early summer.

PLATE XVII

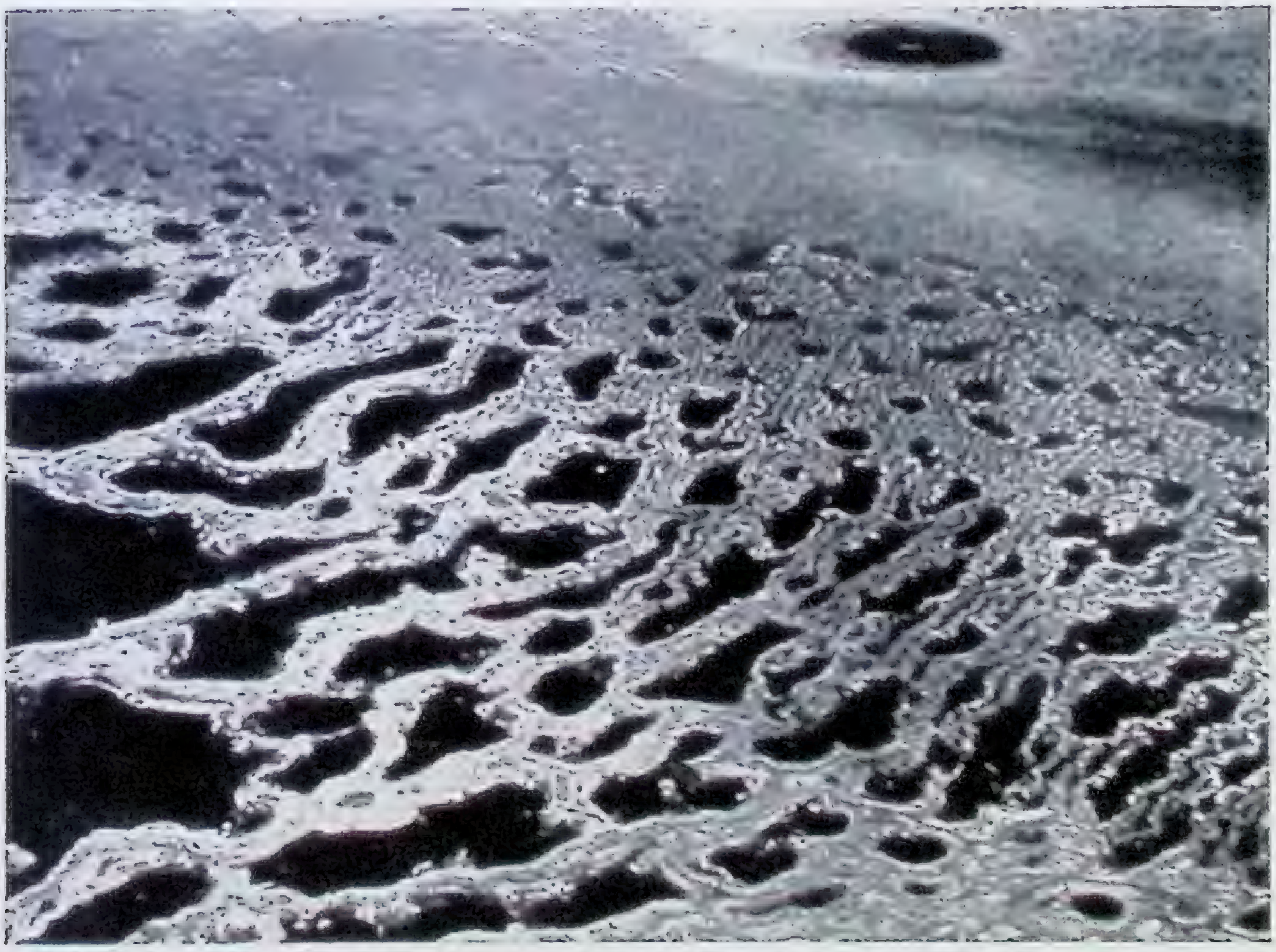


A "ripple-mark" minerotrophic pattern composed of long but narrow, waterlogged flarks, white from sun reflexions but otherwise dark and probably almost devoid of macro-vegetation, alternating with low ridges densely covered by dwarf tamarack. The slope is probably toward the top right corner, where a small black spruce island breaks the pattern. North of Albany River, between Ogoki and Fort Albany

—*Photo A. E. Porsild 1956*

Moreover, we find in certain minerotrophic fens numerous large and less shallow pools. They may look as if formed through coalescence of several narrow flarks (foreground of Plate XVIII), or may have a rounded or irregular outline, mostly unrelated to the slope in their shape (Plate XVII, central part; and Plate II, area *b*). The fen between these pools may be rippled as described above, giving the impression that the pools were formed more recently than the "ripples." It is possible that these pools result from the melting ice structures underlying former "black spruce islands," which then would have collapsed entirely. We did not look for remains of spruce in the few fen pools we were able to reach on the ground. Except for such hypothetical examples, the conspicuous pattern formation in northern peatland (Sjörs, 1961*c*) is certainly not the result of earlier permafrost (as suggested by Hamelin, 1957) but is a general feature of the subarctic, and largely also of the main boreal zone. There is no conclusive evidence that at any time during the post-glacial period, the climate was much colder than at present. In Sweden, where the winter climate is more favourable than in most other boreal countries, the minerotrophic peatland is frequently and conspicuously patterned with "flarks" as far south as Västmanland (Lundqvist, 1932, pp.77–78, 80; Sjörs, 1948, pp. 202, 263, etc.; 1958, pp. 91–92) and S. W. Värmland (Fransson, 1958), i.e., no less than seven degrees of latitude south of the southern limit of palsas (Lundqvist, 1951*a*, p. 224, Ruuhijärvi, 1960, p. 223), which are the only form of permafrost structures reaching Fennoscandia. There is no evidence that permafrost has ever occurred farther south during any phase of the post-glacial time. The winter temperature in the southernmost part of the range of minerotrophic flarks in Sweden is about 10°C warmer than in the palsa area, and equals that of Toronto, Canada. Ombrotrophic peatland is generally patterned even farther south and west in Europe, and patterns occur, for instance, in the British Isles (Osvald, 1949; Ratcliffe and Walker, 1958), where even seasonal soil frost is practically unknown. As discussed elsewhere (Sjörs, 1946, pp. 56–65; 1948, pp. 263, 289; 1950*b*, p. 210; 1961*c*; this paper, Lundqvist, 1951*b*; Ruuhijärvi, 1960, etc.), the patterns seem not to depend on frost (nor on solifluction) but are the result of local cessation of peat formation in waterlogged sites. Hence the formation of

PLATE XVIII



Minerotrophic peatland showing two intergrading patterns, due to extensive fen-pools and very narrow flarks. In the foreground, the fen-pools are close and orientated; in the middle area, they are more widely spaced, their shapes unrelated to the slope. A round black spruce island with a collapsed centre in the background. North of Missisa Lake

—*Photo A. E. Porsild 1956*

patterns is a hydro-topographical and ecological phenomenon, which grows in importance and extends to minerotrophic peatlands under the main boreal and subarctic types of climate but is not the result of very cold winters nor of earlier permafrost. A slightly different opinion is recently advanced by Allington (1962).

Variability in Minerotrophy and pH

Unlike the conditions in the Hawley Lake district (Sjörs, 1961*b*), where practically all minerotrophic areas are strongly calcareous and where less calcareous fens were seen only in narrow ecotones toward the ombrotrophic areas, there exists in the Attawapiskat River area much peatland where minerotrophy is weak (p. 65). We have already mentioned such conditions in the "seepages" on the bogs (p. 79). Weak degrees of minerotrophy also occur along brooks that are chiefly fed by bog water (through the seepages), along transitions toward ombrotrophic areas, and very likely over much of the proximal (upper) parts of the minerotrophic areas in general. Weak minerotrophy is also evident in some of the better-drained wooded peatland, and also in wet patches surrounded by wooded peatland.

TABLE 4

Field determinations of pH (glass electrode) in water from minerotrophic peatland

POOR FEN (excluding the sites in Table 3)		
61.	Attawapiskat River 2 miles downstream, S. side, first *Equisetum silvaticum* on edge of ombrotrophic bog	4.4
79.	Attawapiskat River 2 miles upstream, S. side. Water-saturated "moat" inside horseshoe-shaped "black spruce island," doubtfully minerotrophic. *Eriophorum russeolum*, *Scheuchzeria*, *Carex paupercula;* drowned black spruce	4.5
80.	Brook coming from preceding, breaking through the "black spruce island." Dead black spruce, *Sphagnum riparium*	5.2
77.	Near edge of the "black spruce island" on the outward (northern), lower side, only 3 m from no. 78	5.4
85.	Attawapiskat River 2.5 miles downstream, S. side. Wet area in wooded fen (tall *Larix*, *Salix*, *Alnus rugosa* v. *americana*, etc.) with *Calla palustris*, *Carex canescens*, *Sphagnum riparium*	4.1
56.	Attawapiskat River 2 miles downstream, S. side. Flark-pool in narrow transition (ecotone) between ombrotrophic bog and rich fen. *Carex limosa*, *chordorrhiza*, *Equisetum palustre*, *Menyanthes*, *Utricularia intermedia*, *Eriophorum gracile*, *Sphagnum parvifolium*, *Jensenii*, *Drepanocladus procerus*, etc.; adjacent *Betula pumila* v. *glandulifera*, *Arethusa bulbosa*, *Tomentypnum nitens* v. *falcifolium*	5.1
RICH FEN		
57.	A few metres from preceding. Transitional between poor and rich fen. Additional species, e.g., *Scirpus hudsonianus*, *Juncus stygius* v. *americanus*, *Utricularia minor*, *Sphagnum subsecundum*, *Riccardia pinguis*, *Drepanocladus badius*, *Scapania paludicola*, *Dicranum leioneuron;* adjacent *Sphagnum riparium*	5.8
58.	Adjacent flark-pool, a few metres from preceding. Moderately rich fen. Additional species, e.g., *Potentilla palustris*, *Carex leptalea*, *livida* v. *Grayana*, *tenuiflora*, *Eriophorum viridi-carinatum*, *Drosera linearis*, *Scorpidium scorpioides*, *Calliergon trifarium*, *Drepanocladus revolvens* (s. str.), *uncinatus*, *Campylium stellatum*, *Tomentypnum nitens* s. str. (*T. n.* v. *falcifolium* still present, the two well separable), *Sphagnum Warnstorfianum*, *teres*, the fungus *Mitrula paludosa*	6.5

59.	Large pool farther inside the rich fen. Additional species, e.g., *Calla palustris, Triglochin maritimum* (agg.), *Sparganium minimum, Salix pedicellaris* v. *hypoglauca, Pedicularis parviflora, Eleocharis calva*	6.1
60.	Another large pool. Additional species, e.g., *Epilobium palustre, Carex lasiocarpa* v. *americana, diandra, interior, heleonastes, Drepanocladus vernicosus, Meesia tristicha, Sphagnum contortum*	7.1
78.	Attawapiskat River 2 miles upstream, below 79–80 and above 81. Only 3 m from the acid site 77 (*see* above). Rich fen, *Platanthera* (*Habenaria*) *dilatata* at sampling spot	6.9
81.	Edge of large "flark" below preceding. *Scirpus hudsonianus, Juncus stygius* v. *americanus, Carex livida* v. *Grayana, Utricularia intermedia, Campylium stellatum*, etc.	7.1
82.	Centre of the "flark." Additional, e.g., *Utricularia vulgaris, Eriophorum viridicarinatum, Carex lasiocarpa* v. *americana, Tofieldia glutinosa, Triglochin maritimum* (agg.), *Drosera linearis*. Water analysis no. 3 (Table 1)	7.1
83.	Farther below; wooded fen with *Thuja occidentalis*. *See* list of species, p. 105	6.5
84.	The brook in the lowermost part of the *Thuja* site	7.4

Even the strongly minerotrophic, more or less calcareous, large fens are usually not saturated with lime, at least not so frequently as was seen in the Hawley Lake district. As mentioned (p. 67), there is a wide variation comprising all degrees of minerotrophy in the Attawapiskat River area, although it seems likely from the general chemical composition of the river water (Table 1, No. 4, p. 58) that the variation is due to calcium bicarbonate only, and that no other components of the mineral solutes are appreciably involved. Unlike conditions in silicious districts, as in most of the Canadian Shield and Fennoscandia, minerotrophy is here almost exclusively a question of calcitrophy (p. 59), including the effects of calcium ions on acidity and other properties of the water and peat.

Of the water analyses, No. 3 (Table 1) refers to strongly minerotrophic peatland, showing fairly high calcium and bicarbonate contents and low contents of other ions. The determinations of pH in water from minerotrophic peatland are given in Table 4. Also the samples from seepages and atypical bog-pools (with a few minerotrophic indicators) probably belong in this category (Table 3, p. 80). The seepages with "poor fen" vegetation (Table 3) show pH values between 4.8 and 5.7 and those of the other "poor fen" sites (listed in Table 4) are between 4.1 and 5.4. Some of the latter values are equally low as those found in ombrotrophic sites. The pH range is slightly narrower than that shown for "poor fen" in north-central and northern Sweden (Sjörs, 1952, p. 250), where occasional values as low as 3.8 and as high as 6.5 occur. The somewhat greater frequency of very low values recorded from Sweden may, in part, be due to different determination methods (colorimetric in Sjörs, 1952; electrometric by glass electrode in the present investigation). Also the subsoils are not calcareous in the Swedish areas from which the samples with particularly low values originated.

TABLE 5

Field determinations of pH (glass electrode) in riparian and limnic waters

RIVERSIDE SITES		
28.	Northern bank of Attawapiskat River downstream of the confluence, small spring; water cool, somewhat humous, derived from the bog	6.1
90.	Similar, adjacent spring with stronger flow	7.0
92.	Small brook from another similar spring	7.6
91.	Wet clayey bank, irrigated by 92	8.1
43.	Transect I, 47 m: black spruce forest zone; *Abies balsamea* saplings, *Equisetum silvaticum*, etc.; sample from pit dug to mineral soil at 35 cm	5.6
44.	Transect I, 35 m: white spruce forest zone; additional, e.g., *Cornus canadensis, Pyrola (Ramischia) secunda, Viburnum edule, Mitella nuda, Petasites vitifolius, Equisetum pratense*; sample from pit dug to frozen layer at 32 cm	7.6
45.	Transect I, 17 m: clayey calcareous river bank, with *Primula mistassinica, Carex aurea, Vicia americana, Solidago* spp., etc	8.3
46.	Transect I, 7 m: lower part of bank; *Solidago graminifolia, Deschampsia caespitosa* v. *glauca, Lathyrus palustris, Carex viridula*, etc	8.1
47.	Transect I, 0 m: at water's edge; *Scirpus rubrotinctus, Equisetum fluviatile, Calamagrostis neglecta, Hippuris vulgaris, Potamogeton pectinatus*, etc	8.1
OPEN WATERS		
73.	Lake S. of Muketei River 7.5 miles upstream of the confluence. *Myriophyllum exalbescens, Potamogeton Richardsonii.* July 16	7.7
75.	Brook from preceding. July 16	7.7
76.	Muketei River, adjacent. July 16	7.8
65.	Muketei River at confluence. July 14	7.6
29.	Muketei water in Attawapiskat River below confluence (clear, somewhat humus-coloured). July 8	7.6
48.	Do. (near shore). July 11	7.9
89.	Do. but later: July 23	8.0
88.	Attawapiskat water in Attawapiskat River below confluence (more turbid, less coloured). July 23. Water analysis no. 4, Table 1	8.0
63.	Attawapiskat River upstream of confluence. July 14	8.0
62.	South tributary discharging into Attawapiskat River 7 miles upstream of the confluence with Muketei River. July 14	7.6

Note that a rise in pH took place in the Muketei, probably related to decreasing flow and increasing temperature.

The "rich fen" determinations range from pH 5.8 to 7.4. This is comparable to the pH values of the northern Swedish "transitional rich fen" ("moderately rich fen" in the more recent terminology of Du Rietz, 1954*a*, p. 182), and to the less alkaline of the pH determinations in "extremely rich fen," a comparison that applies precisely also to the vegetational conditions. There are some fen-like wet patches on the clayey river banks below normal flood-level in the Attawapiskat River district. These wet patches are definitely calcareous. Although not peat-forming, they can be regarded as a kind of "extremely rich fen." The single pH value obtained was 8.1 (Table 5, No. 91).

Owing to insufficient time and general inaccessibility, the minerotrophic peatlands were less thoroughly investigated in the field than the ombrotrophic areas, despite the much greater variation in the former. Only a few instances of their structure and vegetation can be reported on, and their subdivision in vegetation types cannot be carried out in any detail.

THE VEGETATION OF POOR FEN

Open Poor Fen

Nearly all minerotrophic indicator plants found in two of the northeastern seepages of the "Transect bog" (just east of the river confluence, (Plates IIIA and VIII) are listed in Table 3, Nos. 67–72, and 25, respectively.

The most frequent of the indicators of minerotrophy in seepages and other wet parts of the ecotones between ombro- and minerotrophic peatland are *Menyanthes trifoliata* and the three minerotrophic *Utricularia* spp. (*U. minor, U. vulgaris,* and particularly the common *U. intermedia; U. cornuta* may also occur but is not an indicator). Another useful indicator of minerotrophy is *Juncus stygius* v. *americanus,* a species reported from few stations (*see* Baldwin, 1958, p. 127; Scoggan, 1957, p. 202) but evidently rather frequent in this area (cf. Dutilly, Lepage and Duman, 1958, pp. 16 and 90, for the east side of James Bay). Other examples are *Eriophorum gracile, Potamogeton alpinus* ssp. *tenuifolius, Equisetum fluviatile, Carex chordorrhiza, Betula pumila* v. *glandulifera,* the orchid *Arethusa bulbosa,* and in certain cases *Scirpus hudsonianus* (*Trichophorum alpinum*). The latter seems to indicate conditions transitional toward the rich fen, in which it is abundant.

The poor fen is usually best characterized by its bottom layer vegetation, i.e., by its bryophytes. Although most of the ombrotrophic species occur also in poor fen (and some, like *Sphagnum papillosum* and *S. Dusenii,* in great quantity), the bryophytes of poor fens include such species as *S. apiculatum, S. Jensenii, S. subsecundum, S. riparium,* and the remarkable suboceanic *S. pulchrum* which was seen repeatedly in the seepages. Another interesting bryophyte is *Drepanocladus procerus* (det. H. Persson; *see* Persson and Sjörs, 1960), a species widespread in Fennoscandia and now reported for the first time for North America. It is not rare in the Attawapiskat River area and was collected also near Hawley Lake. It was seen in wet sites in several poor fens and in smaller quantity in some rich fens. A third remarkable moss is a falcate *Tomentypnum,* identified by Persson with the rare but widespread N. American endemic *T. nitens* v. *falcifolium,* which, however, doubtless is a separate species. It occurs both in the seepages (Table 3, Nos. 70, 25), and in the ecotone toward rich fen (Table 4, Nos. 56–58).

A few of the species mentioned in Table 3 grow abundantly in poor fen but are no indicators of minerotrophy (*Carex limosa, Scheuchzeria,*
falcifolium, which, however, doubtless is a separate species. It occurs both
mineum is doubtful). In a particularly broad and well-developed poor fen area situated between areas of bog and rich fen, *Scheuchzeria* and

Carex oligosperma were recorded as dominants. Many other ombrotrophic plants occur as well, and it seems unlikely that any of the ombrotrophic plants are entirely absent from minerotrophic areas, at least not from poor fen. In a seepage on the bog on the south side of Attawapiskat River, 3 miles downstream of the confluence, pH sample 86 (pH 4.8) and the water for analysis No. 2 (Table 1) were taken. The notes contain the majority of ombrotrophic species (even *Kalmia angustifolia* which is only local on Attawapiskat River); in addition only few minerotrophic indicators were seen, e.g., *Juncus stygius* v. *americanus, Utricularia minor,* and *U. intermedia.*

Wooded Poor Fen

Some poor fen is wooded, due either to very shallow peat or to comparatively good drainage. Black spruce and tamarack are the only trees. The latter here reaches a larger size than in the bogs. Shrubby thickets of willows (species not recorded) and speckled alder (*Alnus rugosa* v. *americana*) occur frequently. The undervegetation is different from that of open poor fens and often resembles that of more or less wooded ombrotrophic bogs (with *Ledum, Chamaedaphne,* the species of *Vaccinium, Rubus chamaemorus, Carex paupercula, C. trisperma, Smilacina trifolia,* etc.), but it contains clearly minerotrophic species such as *Equisetum silvaticum.* Particularly in the wetter parts were found several other minerotrophs, e.g., *E. fluviatile, E. palustre, Carex canescens, C. brunnescens* v. *sphaerostachya, Calamagrostis canadensis, Eriophorum gracile, Menyanthes trifoliata, Potentilla palustris, Lysimachia thyrsiflora,* and occasionally, in very wet sites, *Calla palustris.* The latter sometimes grows in masses in almost pure carpets of *Sphagnum riparium.* The *Sphagnum* flora also includes *S. parvifolium, obtusum, centrale, Girgensohnii, robustum,* and, locally, the more exacting *S. squarrosum, teres,* and *Warnstorfianum.*

There is a gradual transition between moist forest and wooded fen, and some of the species cited above occur also in moist forest near the rivers, where peat-formation is scarcely active. Some of the moist forest sites on mineral substrate are interesting because of their flora, which includes *Carex loliacea* (together with the common *C. disperma;* note that the order of frequency of the two is inverse in Fennoscandia), *C. brunnescens* v. *sphaerostachya, Listera borealis, Ranunculus lapponicus, Cinna latifolia, Platanthera* (*Habenaria*) *obtusata, Stellaria calycantha, Anemone quinquefolia, Botrychium virginianum, Galium triflorum, Sphagnum Wulfianum, Helodium Blandowii,* and so forth. Even though this is a richer assembly of species than the usual, it is not necessarily indicative of truly calcareous conditions (the calcareous subsoil may be near the rhizosphere). "Poor" and "rich" subdivisions of the moist minerotrophic forest can hardly be sharply distinguished. Clearly calcicolous types of wooded fen and moist forest are mentioned below (p. 104).

THE VEGETATION OF RICH FEN

Rich Fen Indicators

As stated above, those parts of the minerotrophic peatlands that are rich fen correspond both to the "moderately rich" and to the "extremely rich" subtype, but we do not possess sufficient material to separate these two subtypes in our areas. The latter subtype is likely to prevail on the large open expanses of fen that we saw from the air but were unable to reach on foot. Interesting features of the flora and vegetation no doubt remain to be discovered in these rich fens, even though the majority of the species observed in rich fen are found also in wet places on clayey, calcareous river banks, which are better explored floristically than are other site types in the lowland (*see* Dutilly, Lepage, and Duman, 1954). However, the flora is rich and varied on all types of wet calcareous sites, and many additions can still be expected both on river banks and in rich fens.

One of the rarest and most interesting of the fen species reported by Dutilly, Lepage, and Duman (1954, p. 52), viz., *Carex heleonastes*, was found also in one of our rich fen sites.

The differential species of rich fen against poor fen are very numerous (cf. Sjörs, 1961*b*). A few species, such as *Carex livida* v. *Grayana* and *C. lasiocarpa* v. *americana*, have yet only been observed in rich fen but are likely to occur also in some of the poor fens. *Scirpus hudsonianus* (*Trichophorum alpinum*) was seen occasionally in the poor fen of the bog seepages and also in the poor-fen ecotone separating the margin of rich fen from bog, but it occurred abundantly only in rich fen. Obligate rich-fen indicators are, e.g., *Carex leptalea*, *C. tenuiflora*, *C. heleonastes*, *Drosera linearis*, *Eleocharis calva*, *Eriophorum viridi-carinatum* (vicarious for *E. latifolium* of

PLATE XIX

A flark, a ridge, and behind the latter, a fen-pool in a minerotrophic area on the south side of the river, 2 miles downstream from the confluence. Vegetation rich in species, among those shown are *Menyanthes*, various *Carex* species, *Eriophorum viridi-carinatum*, *Larix laricina*, and *Betula pumila* v. *glandulifera*. List in Table 6, site A

Europe), *Platanthera* (*Habenaria*) *hyperborea, Salix pedicellaris* v. *hypoglauca, Tofieldia glutinosa,* and *Triglochin maritimum* [agg.; possibly *T. debile* (M. E. Jones) Löve and Löve, 1958, but too immature for sure determination, according to A. Löve]. The first two also grow in rich moist forest and most of the others in riparian sites.

Where the peat is shallow and the calcareous subsoil not very far below the surface, even such species as *Potentilla fruticosa, Muhlenbergia glomerata, Rubus acaulis, Rhamnus alnifolia,* and *Solidago Purshii* may be found occasionally in not too wet places, although they are much more frequent on calcareous mineral soil.

TABLE 6

List of vascular species from two open rich fens. A. E. Porsild's collections and notes included

A: Att. R. 2 miles downstream, S. side (Table 4, nos. 57–60, and surroundings). Nearly complete.

B: Att. R. 2 miles upstream, S. side (Table 4, nos. 78, 81, 82, and surroundings). Less complete than A.

Species	A	B	*Species*	A	B
Andromeda polifolia	+		*Juncus alpinus* ssp. *nodulosus*	+	
Arethusa bulbosa	+	+	*stygius* v. *americanus*	+	+
Betula pumila v. *glandulifera*	+		*Kalmia polifolia*	+	
Calamagrostis inexpansa		+	*Larix laricina*	+	+
Calla palustris	+		*Ledum groenlandicum*	+	
Carex aquatilis		+	*Menyanthes trifoliata*	+	+
chordorrhiza	+	+	*Muhlenbergia glomerata*		+
diandra	+		*Myrica gale*		+
exilis		+	*Pedicularis parviflora*	+	
heleonastes	+		*Picea mariana*	+	
interior	+		*Platanthera* (*Habenaria*) *dilatata*		+
lanuginosa		+	*hyperborea*		+
lasiocarpa v. *americana*	+	+	*Potentilla fruticosa*		+
leptalea	+		*palustris*	+	+
limosa	+	+	*Rhamnus alnifolia*		+
livida v. *Grayana*	+	+	*Rhynchospora alba*	+	+
pauciflora	+		*Rubus acaulis*		+
paupercula	+	+	*chamaemorus*	+	
tenuiflora	+		*Salix pedicellaris* v. *hypoglauca*	+	+
viridula	+		*Sarracenia purpurea*	+	
Chamaedaphne calyculata	+		*Scheuchzeria palustris*	+	
Drosera anglica f. *pusilla*	+	+	*Scirpus hudsonianus* (*Trichophorum alpinum*)	+	+
linearis	+	+	*caespitosus* ssp. *austriacus*	+	+
rotundifolia	+		*Smilacina trifolia*	+	
Eleocharis calva	+	+	*Solidago Purshii*		+
Epilobium palustre	+		*Sparganium minimum*	+	
Equisetum fluviatile	+	+	*Tofieldia glutinosa*		+
palustre	+		*Triglochin maritimum* (agg.)	+	+
Eriophorum gracile	+	+	*Utricularia cornuta*	+	+
russeolum	+		*intermedia*	+	+
virginicum	+		*minor*	+	
viridi-carinatum	+	+	*vulgaris*	+	+
Galium sp.		+	*Vaccinium oxycoccus*	+	

Two incomplete lists of vascular species found in typical open rich fen with "flarks" and drier ridges are given in Table 6.

Of the two most important plant communities that constitute the vegetation of open rich fens, one is found in the water-saturated flarks and in the pools with shallow water, and the other on the low ridges or strings.

Vegetation of Rich Fen Pools and Flarks

In the pools and wet flarks occurs a sparse vegetation, chiefly formed by scattered shoots of *Carex livida* v. *Grayana, C. limosa, C. chordorrhiza, C. lasiocarpa* v. *americana, Menyanthes trifoliata, Equisetum fluviatile,* various *Eriophorum* spp., *Juncus stygius, Drosera linearis, D. anglica* v. *pusilla,* and *Triglochin maritimum.* A few aquatics occur here, among them *Sparganium minimum* and, more frequently, species of *Utricularia.*

The bottom layer is usually poorly developed also with regard to the quantity of the bryophytes; *Scorpidium scorpioides* is the most prominent species here. Growing among the bryophytes and *Utricularia,* or sometimes replacing them, masses of algae occur in the shallow water. In some places iron ochre is produced (by iron bacteria and algae, presumably chiefly desmids). The importance of the oxidative condition brought about by the algae in the shallow pools and flarks has been discussed elsewhere (p. 74). Corrosive oxidation and, in general, active decomposition of plant material cause the growth of the peat to be slow or may inhibit it altogether in the wetter parts of the fen areas. For this reason these peatland areas remain low and continue to be minerotrophic.

A better growth of bryophytes is found in not quite so wet places near the edges of the flarks: *Scorpidium scorpioides, Calliergon trifarium, Meesia tristicha, Drepanocladus intermedius, D. badius, D. procerus, D. vernicosus, Campylium stellatum, Sphagnum contortum,* and so forth. These species are confined to rich fen except *Campylium* and *D. intermedius,* which are also common on wet river banks, and *D. procerus,* which also occurs in some poor fens (*see* above, p. 99).

Vegetation of Ridges in Rich Fen

The ridges or "strings" have not been investigated in any detail. Dwarf tamarack (*Larix laricina*) is usually present and, as mentioned, often abundant enough to impart a characteristic light green tinge to the rich fens in summer (and an equally distinct yellow colour in autumn, according to Porsild), when seen from a distance or from the air. In more southern parts of the lowland (particularly near Moose River) are found extensive "mixed swamp forests" (Hustich, 1955, p. 19) and "tamarack swamps" (Hustich, 1957*b*, pp. 27, 35) covered by closed but low *Larix* forest. A transitional type between these and the wetter, less densely wooded rich fens of our area is seen in Hustich's Fig. 7 (1957*b*). A shrubby understory of *Betula pumila* v. *glandulifera* and some *Myrica gale* is frequently developed. Various sedges (*Carex leptalea, C. tenuiflora,* etc.), *Scirpus caespitosus* and *hudsonianus,* and *Eriophorum viridi-carinatum* are among the numerous field-layer species. The bryophytes are chiefly

PLATE XX

Tamarack fen with small clumps of black spruce arranged along parallel lines. Coastal part of the Lowland, between Moose and Albany rivers

—*Photo A. E. Porsild 1956*

represented by *Sphagnum Warnstorfianum* and *Tomentypnum nitens* s.str., with *T. nitens* v. *falcifolium*, *Campylium stellatum*, *Drepanocladus badius*, and so forth, mainly in the lower parts.

Wooded Rich Fen

Wooded rich fen and rich moist forest occur locally, particularly along brooks, and harbour a rich and varied flora. As reported in Sjörs, 1959 (p. 7), an occurrence of eastern cedar (*Thuja occidentalis*), the northernmost known with certainty (cf. map in Hustich, 1957*b*, p. 23), was discovered near the mouth of a small creek entering the Attawapiskat River from the south, 2 miles above the confluence with Muketei River. Here we noted a large number of cedars, most of them small and shrubby and only very few reaching tree size. One of the largest had recently been cut, probably by Creė Indians among whom the light and durable wood is in great demand. The upper part of the site is a partly wooded fen (water pH 6.5, Table 4, No. 83). The lower part of this fen is drained by the creek (pH 7.4, No. 84), and for this reason is more densely wooded. *Thuja* was nowhere dominant. Another find of *Thuja* is mentioned below.

TABLE 7

List of vascular species from partly wooded, partly shrub-covered rich fen and moist forest (*Thuja* site; *see* Table 4, nos. 83, 84). Nearly complete. Some species included, collected or noted by A.E. Porsild

- *Abies balsamea*
- *Alnus crispa*
  - *rugosa* v. *americana*
- *Amelanchier* sp.
- *Anemone parviflora*
- *Aster umbellatus*
- *Betula pumila* v. *glandulifera*
- *Calamagrostis canadensis* v. *Langsdorffii*
- *Carex aquatilis*
  - *canescens*
  - *disperma*
  - *interior*
  - *leptalea*
  - *loliacea*
  - *media*
  - *paupercula*
  - *tenuiflora*
  - *trisperma*
  - *vaginata*
- *Chamaedaphne calyculata*
- *Chamaenerion angustifolium*
- *Chiogenes hispidula*
- *Coptis groenlandica*
- *Cornus canadensis*
- *Drosera rotundifolia*
- *Empetrum hermaphroditum*
- *Equisetum arvense*
  - *fluviatile*
  - *silvaticum*
- *Galium triflorum*
  - sp.
- *Geocaulon lividum*
- *Glyceria striata*
- *Halenia deflexa*
- *Juniperus communis* v. *depressa*
- *Kalmia polifolia*
- *Larix laricina*
- *Lastrea dryopteris* (*D. disjuncta*)
- *Ledum groenlandicum*
- *Linnaea borealis* v. *americana*
- *Lonicera oblongifolia*
- *Mertensia paniculata*
- *Mitella nuda*
- *Myrica gale*
- *Picea mariana*
- *Platanthera* (*Habenaria*) *hyperborea*
- *Potentilla fruticosa*
- *Ranunculus lapponicus*
- *Rhamnus alnifolia*
- *Rosa blanda*
- *Rubus acaulis*
  - *chamaemorus*
  - *pubescens*
  - *strigosus*
- *Salix pedicellaris* v. *hypoglauca*
  - *planifolia*
- *Scirpus hudsonianus* (*Trichoph. alp.*)
- *Smilacina trifolia*
- *Sorbus decora*
- *Thuja occidentalis*
- *Trientalis borealis*
- *Triglochin palustre*
- *Vaccinium microcarpum* (*Ox. m.*)
  - *myrtilloides*
  - *oxycoccus* (*Ox. q.*)
  - *uliginosum*
  - *vitis-idaea* v. *minus*
- *Viburnum edule*
- *Viola adunca* v. *minor*
  - *renifolia* v. *Brainerdii*

Other trees and shrubs growing on this site include black spruce, tamarack, balsam fir, *Alnus crispa*, *A. rugosa* v. *americana*, *Sorbus decora*, *Betula pumila* v. *glandulifera*, *Viburnum edule*, *Juniperus communis* v. *depressa*, *Myrica gale*, *Rhamnus alnifolia*, *Potentilla fruticosa*, etc. A nearly complete list of the vascular species from this site is given as Table 7, which includes both the wooded fen and the moist forest.

The following bryophytes were noted in this wooded rich fen: *Sphagnum Warnstorfianum*, *contortum*, *centrale*, and *parvifolium*, *Riccardia* *pinguis, Drepanocladus revolvens* s.str., *Campylium stellatum, Calliergon stramineum, Aulacomnium palustre, Tomentypnum nitens, Pleurozium Schreberi.* Also the fungus *Mitrula paludosa* was seen. It occurs also in open rich fen (Table 4, No. 58); pH was 6.5 in both places.

Riparian Rich Fen

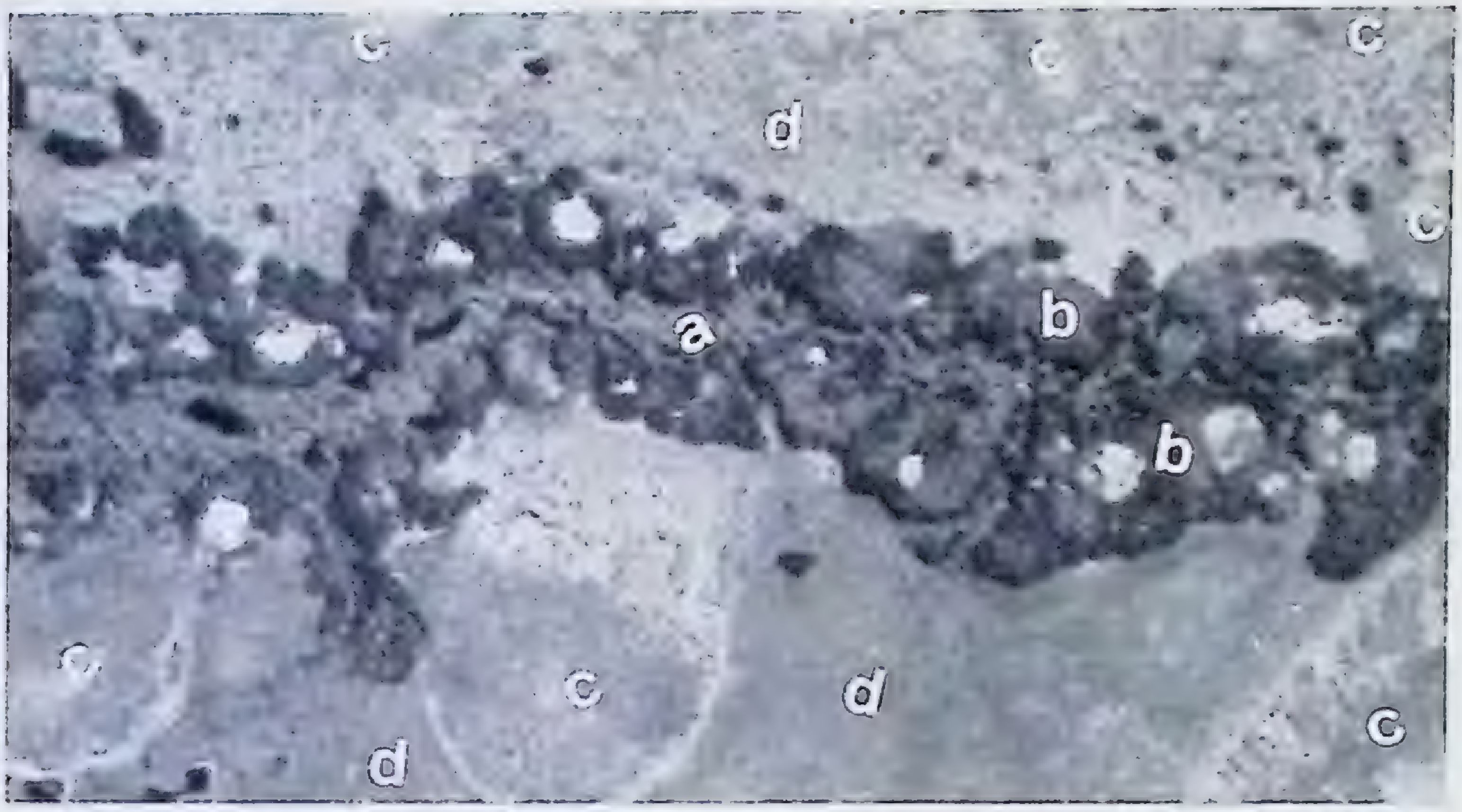
As mentioned above, the fen-like but not peat-forming wet patches on the clayey river banks have the richest fen vegetation occurring in the area. Besides fen species, this vegetation contains components of the types of vegetation which cover less water-saturated, frequently eroded calcareous clay and clayey till on the river banks.

Near Transect II, two small springs irrigate a gently sloping part of the river bank, which is submerged during the spring flood. Close to the springs, a low herb community of *Lobelia Kalmii, Parnassia parviflora,* and a multitude of other species occur on the bare moist clay. The more fen-like lower part of the irrigated area is overgrown by various *Carex* species, among which *C. lanuginosa* is usually dominant; other prominent or interesting species are *Carex aurea, C. Buxbaumii, C. Crawei, C. interior, C. viridula, Deschampsia caespitosa* v. *glauca, Iris versicolor, Juncus Dudlei, Parnassia palustris* v. *neogaea, Pedicularis groenlandica, Platanthera (Habenaria) hyperborea, Poa palustris, Potentilla fruticosa, Stellaria crassifolia, Tofieldia glutinosa, Triglochin maritimum* (agg.). The bryophytes include *Philonotis fontana, Drepanocladus intermedius, Hypnum Lindbergii, Bryum pseudotriquetrum,* and *Campylium stellatum.*

From a similar site just upstream from Transect I were noted: *Aster simplex, Carex interior, C. lanuginosa, C. viridula, Deschampsia caespitosa* v. *glauca, Eleocharis calva, Equisetum palustre, E. variegatum, Glyceria striata, Juncus alpinus* ssp. *nodulosus, J. nodosus, Lobelia Kalmii, Lycopus americanus, Parnassia parviflora, Pinguicula vulgaris, Primula mistassinica, Prunella vulgaris* v. *lanceolata, Ranunculus reptans, Salix* sp., *Solidago graminifolia, Stellaria crassifolia,* and *Viola* sp., with the same bryophytes as the preceding site (except *Bryum*). The water pH was 8.1 (Table 5, No. 91).

Seven miles upstream from the Attawapiskat-Muketei junction, an unnamed although fairly large tributary enters the Attawapiskat from the south. We called it "Cedar Drift River" because we found some *Thuja* twigs in flotsam deposited by spring floods. The area drained by this stream extends 60 miles to the south (approximate position: Latitude 52° 20′ to 53° 5′ N., Longitude 85° 30′ to 50′ W.). The river banks consist of glacial till and weathered rock derived from limestone or calcareous sandstone; the bed-rock is exposed in the bank and the river bottom near a small rapid. Above the rapid the river is slow and strongly meandering, and its banks are partly shrub-covered (alders, willows, *Potentilla fruticosa,* etc.). Here we noted several very small springs irrigating patches of interesting vegetation containing calcicolous dwarf species such as *Carex microglochin* and *Eleocharis pauciflora;* also *Juncus albescens, Ranunculus septentrionalis,* and *Poa alpina* were observed here.

PLATE XXI



Vertical view of area *c*, Text Fig. 2 (p. 49), northeast of the river confluence. (*a*) Meandering brook. (*b*) Double rows of black spruce islands along the brook; the white patches are either dry, lichen-covered hillocks, or bright *Sphagnum* carpets. (*c*) Mostly small, ombrotrophic bogs. (*d*) Tamarack fen without micro-pattern —*Photo by R.C.A.F.*

"BLACK SPRUCE ISLANDS" IN FENS

In the peatland landscape of the central parts of the Hudson Bay lowland, the roundish "black spruce islands" are most striking features when seen from the air. Much study was devoted to them by both Porsild and Hustich during the flights in 1956, and several close-up colour photographs were taken both in 1956 and 1957 in order to show their structure. A few have been published in Hustich, 1957*a* and *b*, and in Sjörs, 1959 and 1961*c*.

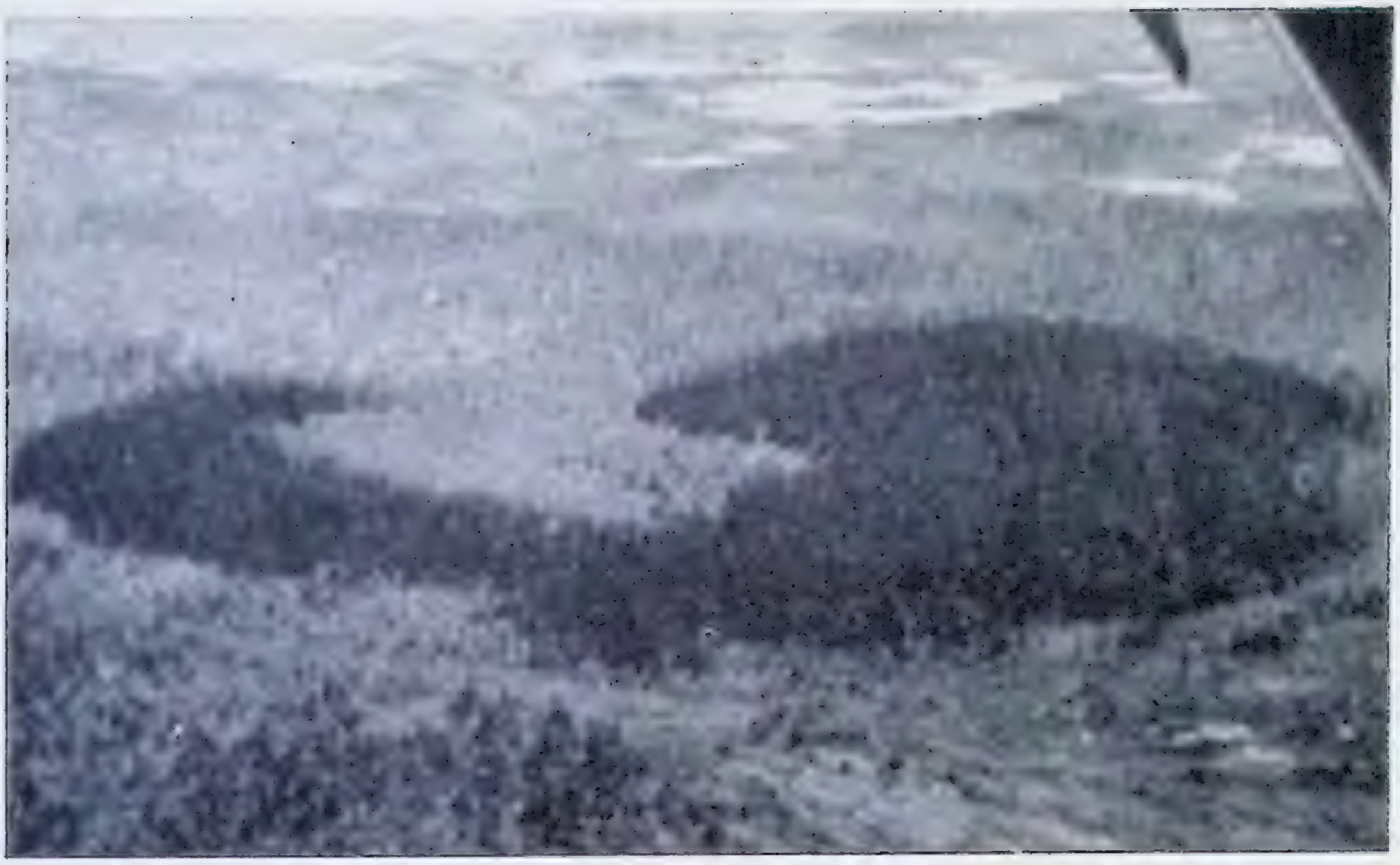
These conspicuous "islands" are probably absent in the northern and southern parts of the lowland. Other types of permafrost hillocks occur in the north, e.g., the "palsas" described from ombrotrophic bogs in the Hawley Lake area (Sjörs, 1959, pp. 15–17; 1961*b*, pp. 18–28; 1961*c*, Figs. 11–12). As far as we know, the "black spruce islands" are a feature of the northern part of the main boreal zone (or its transition toward the subarctic proper), developed under a continental climate with summers favourable for tree growth but with very cold winters. Their distribution is unknown but reaches southern Alaska (Cook Inlet area, and along the Alaska Highway near the Yukon border, according to Drury, 1956, p. 75). Their presence appears to be associated with certain topographic features, such as flat, smooth, and extensive but shallow peatland; possibly slightly mobile subsurface water may have something to do with their genesis. In the Hudson Bay lowlands they chiefly occur in two rather dissimilar types of minerotrophic areas, i.e., in series paralleling certain brooks, or irregularly scattered in large open fen expanses. Along the streams they are often very extensive and more or less confluent and sometimes have lichen-covered summits resembling palsas; in the open fens they are usually smaller and characteristically "rain-drop-shaped" with tapering "tails" pointing in the direction of the flow of water. Irregularly elongated, scattered "islands" may occur in some peatland without a distinct slope (Fig. 6 in Coombs, 1954, an oblique aerial photograph by H. C. Hanson, from about 15 miles north of Attawapiskat River).

The only "black spruce island" visited, half a mile upslope (S.) from the *Thuja site* (p. 97; Plate XV, area *c.* p. 91, and Plate XXII), is now horseshoe-shaped, about 230 m across, with a large, nearly central, crater-like depression evidently formed by the gradual collapse of the "island" because of melting. On the inside of the rim, facing the central depression, drowned black spruces are partly submerged in a "moat" with shallow water, locally being buried in freshly formed soft peat. The "moat" (cf. Drury, 1956, p. 21) is in this case rapidly colonized by *Eriophorum russeolum* and some *Carex paupercula* and *Sphagnum*. The older parts of the depression are overgrown by bog vegetation, seemingly ombrotrophic (but the "moat" may be slightly minerotrophic, Table 4, No. 79, p. 96). Below superficial medium humified *Sphagnum* peat, we found, at 9 to 35 cm, a less humified, light-coloured *Sphagnum* peat formed under very wet conditions and containing rhizomes (probably of *Scheuchzeria*) and in lower parts possibly also remains of *Rhynchospora alba* (uncertain). Below 35 cm was again medium humified bog-peat, but the pit filled up with water so rapidly that we were unable to reach unquestionable remains from the "spruce island" period. Unfortunately, we had not brought the peat-borer with us and could not return to the place.

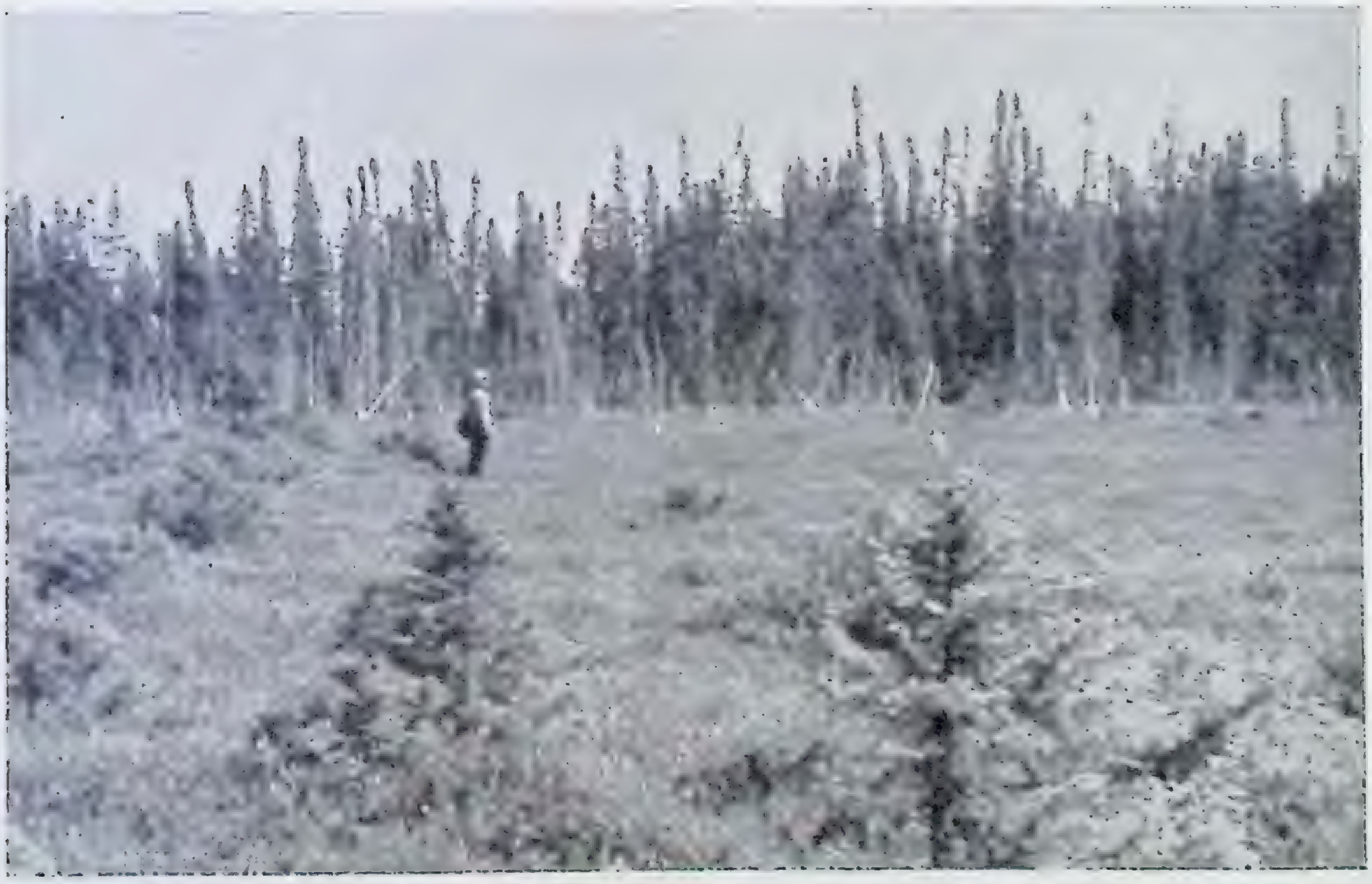
The black spruce covering the standing rim of the "island" is crowded but partly dead. Most of the trees are leaning outward, owing to large fractures resulting from the gradual collapse, in particular the melting of the edge. The "island" rises rather abruptly from the inside depression as well as on the downslope side (facing a fen); the highest point of the rim being about seven feet above the fen. The interior is covered by a low but very dense black spruce stand, with a poor undergrowth of *Ledum groenlandicum* and some *Rubus chamaemorus* and *Vaccinium vitis-idaea* v. *minus*. *Chamaedaphne* seems to be absent here. In the bottom layer grow *Ptilidium ciliare, Pleurozium Schreberi, Cladonia rangiferina,* and *Dicranum polysetum* (= *undulatum*). There are no *Sphagna* at present, but a stratum of *Sphagnum* (possibly *fuscum*) was found 40 cm below the surface; all the rest of the peat is highly humified, at least down to the permafrost struck at 70 cm.

The run-off from the "crater" gives rise to a small brook which has cut a narrow passage through the rim of the "island." Dead spruces were noted along this narrow ditch, with *Sphagnum riparium* growing along the brook itself. The brook-water (Table 4, No. 80, p. 96) runs into the flarks of an open fen downslope from the "island." This fen also receives other, seemingly more calcareous tributaries and is strongly minerotrophic (Table 1, water analysis No. 3, p. 58; plant list in Table 5, No. 2, p. 98).

PLATE XXII



A. The investigated horseshoe-shaped black spruce island, seen toward the southwest; also shown on Plate XV (*c*). Surrounding mostly wooded bog; bottom right a rich fen (Plate XV, *d*)



B. The same "island" (Plate XXIIA), seen from the centre. Note dead black spruce along the frozen and elevated rim of the densely forested "island."

The presence of permafrost isolated in "black spruce islands" in the central Hudson Bay lowland, far beyond the southern limit of continuous permafrost, is remarkable, even more so than is the occurrence of isolated bodies of permafrost in the "palsas" of the somewhat more northern truly subarctic region. There is an extensive literature on the palsas in North Europe (where palsas are probably the only type of permafrost occurring in the subarctic region). The most important recent treatments seem to be Lundqvist, 1951*a* (in Swedish but with a brief abstract in English); Ruuhijärvi, 1960 (pp. 222–230, 237–240, 289); Kats, 1948; and Pyavchenko, 1955; although there may be other papers in Russian, unknown to the author. Lundqvist's investigation was discussed at some length in a recent paper (Sjörs, 1961*b*, pp. 25 and 27), and for the present it will be sufficient to summarize Lundqvist's discovery that the lower parts of the frozen core of a palsa are formed by alternating sheets of pure ice and frozen peat. The ice crystals attract water from outside during freezing, thus strongly augmenting the volume of the palsa by the freezing of the water that is drawn into the body of the palsa by suction, from below or from the outside.

In eastern North America, palsas (often called mounds) are known to occur in the northern half of the Labrador peninsula (Hare, 1959, p. 32), in particular on the east coast (Hustich, 1939; Wenner, 1948); west and southwest of Ungava Bay (Potzger and Courtemanche, 1955; Allington, 1959); and near the west coast on Great Whale River (Hustich, 1950, p. 38). Palsas are also found in the subarctic parts of Ontario and Manitoba (Hustich, 1957*b*, p. 38; Sjörs, 1959, 1961*b*; Radforth, 1955; Ritchie, 1957, p. 432; 1960*c*, p. 783). Farther west they are reported by Porsild (1945, 1951) from the Yukon-Mackenzie boundary, at high elevation (4,200 to 4,500 feet), and by Moss (1953, pp. 462, 468–469; 1955, p. 534) from moderately elevated, boggy plateaux in N.W. Alberta. Some palsas are treeless; others are scantily covered by trees, in N. America chiefly low black spruce. Permafrost is not continuous in the peats of the palsa zone. Evidently this type of mound of medium height cannot be built up without access to liquid water from the subsoil. From areas where permafrost[1] is continuous in undrained soil, true palsas (of medium height) are not known[2], but peatlands frequently form elevated frozen platforms with uneven surface. Local access of liquid subterraneous water may result in formation of very high pingos (Porsild, 1938).

As stated above, the "spruce islands" represent a more southern variety of frozen mound. Contrary to the palsas, they have not been reported from the Quebec-Labrador peninsula, nor from North Europe, where, in the zone allowing dense conifer growth on peat, the winters are not cold enough for any occurrence of permafrost structures.

Drury (1956, p. 76) and Hustich (1957*b*, p. 26) both emphasize the importance of "layering," i.e., vegetative reproduction by rooting branches, for the development of "black spruce islands," *Picea mariana* being better adapted for this way of growth than are other boreal American conifers. They think that a frozen hillock was first formed, and then colonized by the black spruce because of better drainage than in the surroundings.

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[1] The Swedish word *tjäle* is sometimes erroneously given as a synonym of permafrost (which is not known with certainty from Sweden, except in the palsas in the extreme north of the country). *Tjäle* simply means frozen soil, which is seasonal in Sweden.

[2] Lower types of mounds replace them to the north in U.S.S.R. (Kats. 1948; Pyavchenko, 1955; cited by Ruuhijärvi, 1960, p. 238). The mounds reported from interior and northwest Alaska by Hanson (1950) are low hummocks, resting on probably continuous permafrost.

A. E. Porsild (in litt.) has expressed the following view on the development of the "black spruce islands" of our area:

> The origin of these 'spruce islands' is not clear. It would seem likely, however, that they developed during a period with a colder climate. Many spruce 'islands,' occurring more or less isolated, in large fens, are circular or somewhat oblong. In many spruce 'islands' the centre has collapsed so that they now appear ring-shaped. The rim is forested and the centre a tree-less, wet bog. Often a shallow, moat-like depression circles the 'island.'
>
> The ring-shaped black spruce 'island' is clearly the result of collapse or thawing out of its former permafrost core. The rim, which still contains remnants of a permafrost core, is often fractured or broken up into irregularly shaped blocks by deeply eroded fissures; the moat is almost certainly caused by the settling of the rim into the soft, no longer frozen, mineral subsoil.
>
> The ring-shaped stage of the black spruce 'island' resembles the last stages of pingos described from the arctic coast of Mackenzie district and Alaska by Porsild (1938). The resemblance, however, is only superficial, because the genesis of the true pingo, as described by Porsild (l.c.), is quite different.

Evidence from "nivation hollows" and permafrost lenses at depths of 20 to 40 feet or more, in central Quebec-Labrador (Henderson, 1959, pp. 70–80), supports the idea of one or more former colder periods.[1]

The existence of an earlier period with a colder climate has also been postulated by Hamelin (1957) to explain "flark" formation in central Quebec (*see* discussion on p. 94). Considering the former greater extent of Hudson and James bays (the Tyrrell Sea, Lee, 1960), it is likely that near this sea, springs and summers were cooler in the earlier part of the time elapsed since the general climate deterioration about 2,500 years ago than they are at present. A much colder climate than at present seems to be rather unlikely, however; and Terasmae did not document it as such in his pollen diagram (Terasmae and Hughes, 1960). The climatic fluctuations cannot possibly have been strong enough to have pushed general permafrost southward into the Attawapiskat River area (nor into south-central Labrador-Quebec) at any part of the post-marine time.

The present positive minor fluctuation in the climate has caused the subarctic palsas and also our "black spruce islands" to melt to a considerable extent, and they are probably unable to regenerate under present conditions. Conditions for the local permafrost that they represent were probably somewhat more favourable (i.e., the climate was slightly more severe) during the unknown period or periods in which they originated.

The reasons for the black spruce islands becoming and remaining perpetually frozen must be partly different from those advanced for the palsas (Lundqvist, 1951*a*; Sjörs, 1961*b*). The sites corresponding in position to palsas are not perennially frozen in the Attawapiskat River area, and the physiographical and micro-climatical character of the two structures differs considerably. The palsa, being treeless or nearly so, and generally lacking snow cover, is exposed to high winds and strong radiation of heat in winter; the black spruce island, on the other hand, is covered by forest notable for its density. Despite their more southern occurrence, black spruce islands are frequently much larger than palsas, being often a few hundred metres across, i.e., about five times or more the average diameter of palsas (although black spruce islands of small dimensions also occur). The height, which is usually three to ten feet in palsas (occasionally more in Europe), is probably similar in black spruce islands.

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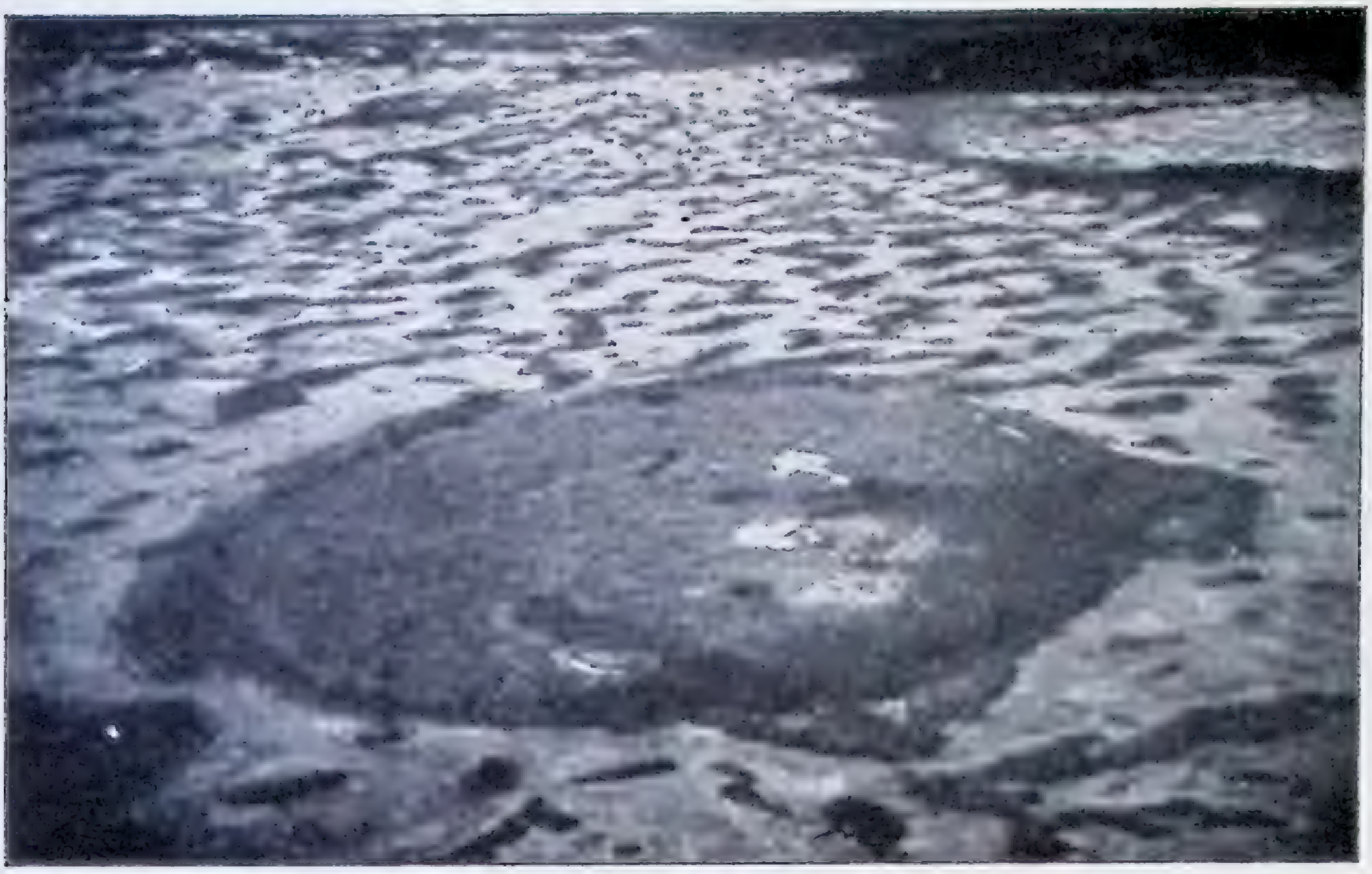
[1] However, the solifluction in "nivation hollows" is probably more dependent on intense wetness than on intense cold. The accumulation of snow is a consequence of, as well as an agent in, the formation of the "hollows." The snow provides not only additional weight and wetness, but also thermal insulation, which restricts the efficiency of the freeze-and-thaw process for solifluction. The interpretation of permafrost lenses at great depth is also open to discussion. Moreover, the elevated Knob Lake area is, even in present time, climatically very unfavourable (Allington, 1962) and is not far from the present outliers of superficial permafrost.

In the heavily forested main boreal and lower subarctic zones of Fennoscandia, there appears very locally on former clearings and burns an extremely dense young forest of Norway spruce (*Picea abies*) which, if thinning is neglected, develops into an over-crowded stand of weak trees, termed in Swedish "stavagranskog," i.e., "stick spruce forest." This undesirable type of stand is notorious for the late thawing of the soil, which is partly responsible for its poor growth (Ronge, 1928). The heavy and prolonged ground frost is believed to result from the thin snow cover inside the stand, most of the snow being caught by the dense spruce canopy, from which it disappears by melting or evaporation. Only a small fraction of the solar radiation energy reaches the ground in spring and summer, retarding consequently, the thawing of the frozen soil. To some extent this applies to all dense coniferous forests (Ångström, 1936), but the effects will be extreme only in very dense stands. There has been some discussion about the question whether the snow effect is of any importance when the insulating humus cover is thick (Berg, 1929; Ronge, 1929). However, an insulating humus cover influences both access and loss of heat to about the same degree, whereas the snow cover only influences the loss of heat in winter.

Judging chiefly from aerial photographs, the stands of black spruce on the "islands" are usually extraordinarily crowded. This species of spruce frequently has dense, long, persistent branches, which may be able to collect snow very effectively particularly around the perimeter of the stand. As wind shelter is provided in the interior of a dense stand, little snow will reach the ground.

The problem of the genesis of the black spruce islands also involves the two questions: why such "islands" have developed only in special sites on the fens, and why permafrost is not general in dense spruce stands. It is possible that the origin of the "islands" was dependent in some way on water mobility. Because of better oxygen and nutrient supply to the roots, black spruce stands may have grown more densely near moving water. The ground ice may also have increased more readily in thickness if water was easily available. (As mentioned above, available liquid water is a prerequisite for the growth of certain frost mounds in true permafrost regions where free ground water is normally absent; *see* Porsild 1925, 1938.) The development and permanency of a raised, frozen black spruce island also require absence of fire, a condition which is rarely fulfilled for a very long period in continuous forest, particularly on dry or mesic soil. In our area, also the bogs, at least their more or less wooded marginal parts, have burnt repeatedly. The probability of fire is much lower for an



A large burnt-over black spruce island. Coastal lowland, north of Attawapiskat River

isolated island in a wet fen. Nevertheless, burnt "black spruce islands" were observed, and it seems likely that after a fire, the ice core will melt and the "island" will collapse before the spruce has a chance to regenerate. More numerous instances were seen of collapsing unburnt black spruce islands, with dead, leaning trees either peripherally or in central parts, as stated by Porsild (above, p. 111). Eventually a "crater" occupied by a large pool will result, but the origin of the pools occurring in the fens has not been investigated.

The present conditions in black spruce islands are ombrotrophic, and the vegetation of the example seen is regarded as wooded bog vegetation without minerotrophic indicators. Very little peat, however, is actually formed, and probably minerotrophic peat is sometimes not far under the surface. Most of the minerotrophic strata must be frozen, but it is not impossible that in certain cases minerotrophic layers may be reached by the annual thawing from above and may even be within reach of plant roots. Therefore the possibility cannot be excluded that minerotrophic indicators could persist in some black spruce islands in spite of the present ombrotrophic conditions.

Black spruce islands in sloping fens frequently have an ombrotrophic downslope "tail," easily noted from the air. The "tail" contrasts by a brighter, more yellowish or reddish light-brown colour against the surrounding darker, olive green, usually "rippled" fen (Sjörs, 1959, Fig. 2). The "island" divides the flow of minerotrophic water into two parts, which cannot unite again immediately, leaving the tapering "tail" between them for some distance. The "tail" is slightly elevated and is drier than the fen, for it receives only water from the rain and snow falling on it. The "boundary of minerotrophy" (Plate III B) is often very sharp in the basal part but naturally less sharp at the tip of the "tail."

REMARKS ON STRATIGRAPHY

A few pits and borings have been made in three places in the Transect bog at the Muketei-Attawapiskat river junction. The peat samples collected have been passed to Dr. J. Terasmae of the Geological Survey of Canada and partly worked up by him (Terasmae and Hughes, 1960). Also a few samples for radiocarbon dating were taken. This work has not yet been completed, and its bearing on the vegetational history of the area of investigation will not be discussed here. Only a few remarks on the stratigraphy and development of the peat deposits will be made. The levels are referred to the summer low water-level of the river.

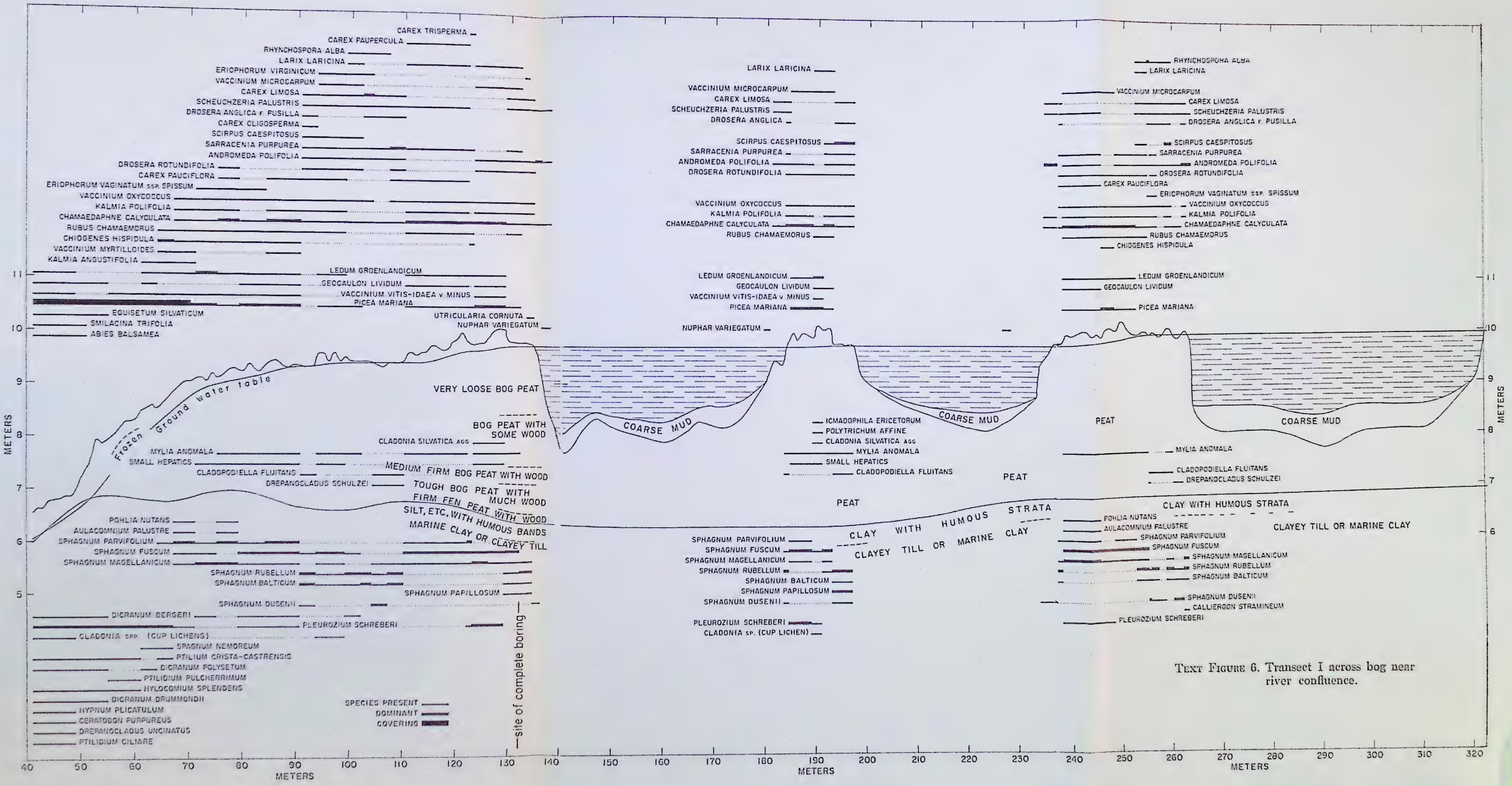
Profile in Transect I

Transect I was planned as a cross-section, but borings could be carried out only from the riverward margin to the third large bog-pool; the rest of the bottom profile shown in Text Fig. 4, p. 72, is conjectural. Despite the moderate thickness of the peat, the borings were time-consuming because the peat was very firm and tough in its lower part.

The peat deposit rests on marine calcareous clay or calcareous clayey till (separable with difficulty in borings). The following more or less arctic marine molluscs have been found outwashed on the river bank (det. Frances J. E. Wagner): *Hiatella (Saxicava) arctica* (dominant), *Portlandia (Yoldia) arctica, Clinocardium ciliatum, Macoma calcarea,* and *Mya truncata.*

The following sequence (from bottom upward) was found in Transect I at 132 m from the river, near the riverward edge of the first large bog-pool. From the clay surface at 597 cm up to 630 cm, the deposit consists of clayey and silty very fine sand with humus bands, evidently representing an alternation of humus and river deposits similar to that seen on islands in the river (Sjörs, 1959, Fig. 6). The lowermost humus band at about 599 cm is peaty and contains remains of wood. It seems to be derived from the first wooded fen that colonized the area, after it had passed a short period as intertidal salt marsh, which evidently did not leave appreciable organic deposits in this place. The surroundings of the river must have been flooded repeatedly until the river-bed was eroded and widened enough to allow the high waters to pass without so much flooding.

From 630 cm begins the continuous peat deposit which up to about 707 cm is highly decomposed and contains a considerable amount of wood. This peat probably originated in a wooded fen. The last visible fine sand is at 637 cm, but feeble silting may reach higher. The cessation of severe flooding thus was at 637 cm above present summer low water-level, whereas the general silting from the highest recent floods reaches 7 m or higher. These floods are caused by exceptionally severe ice jams in the river (Sjörs, 1959. p. 7; the uppermost ice scars on white spruce trees along present river banks occur at 850 cm). Either the ice jams or the peaks of springtime water-



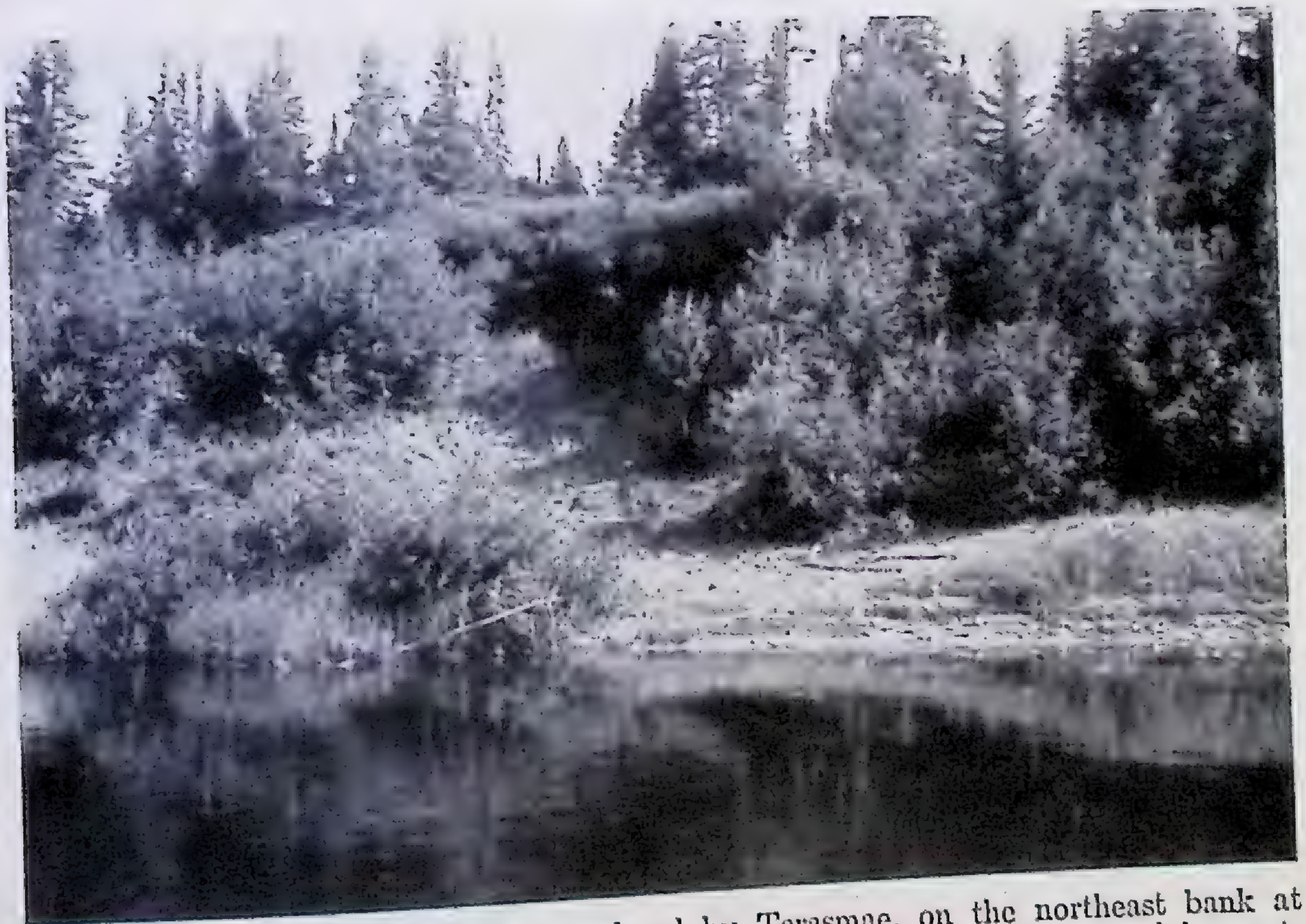
TEXT FIGURE 6. Transect I across bog near river confluence.

flow were less severe during the xero-thermic period, a prerequisite for the subsequent ombrotrophic development so close to the river. The first *Sphagnum* remains were noted at 639 cm, which is immediately above the uppermost visible fine sand. The limit of minerotrophy in a vertical sense, i.e., the level where the minerotrophic influence was no more active, must be considerably higher.

After the flooding had ceased entirely, the wooded fen thus gradually developed into a wooded ombrotrophic bog. The woody vegetation at first covered a larger part of the bog than at present, or possibly the whole bog. As the drainage was not better than now (the bog was less up-domed), it is inferred that the development of extensive wooded fen and wooded bog took place during a xero-thermic period, which may be identified with the "pine period" or Q-3 of Potzger and Courtemanche (e.g., 1956). However, a somewhat similar development still takes place near the estuaries of large rivers in the Hudson Bay Lowland (Ritchie, 1957).

The wooded fen and, later on, wooded bog grew only slowly in height, leaving highly humified, dark remains, which are particularly tough and rich in wood between 672 and 692 cm, corresponding to fairly dry conditions. The content of wood decreases above 692 cm, and at 707 cm there is a transition to less wooded, more open bog. The woody remains have not been determined to species.

PLATE XXIV



Site of the peat profile micro-analysed by Terasmae, on the northeast bank at the river confluence. The bog peat is drained and compressed, covered by scattered black spruce of tree size. Due to a very recent clay-slide (left), a fresh section of peat is exposed on the top of the bank. The shrubs are chiefly aspen (*Populus tremuloides*). —*Photo G. Sjörs*

The stratum between 707 and 740 cm is medium humified and medium firm. Above 740 cm the peat is less firm (but woody remains do occur, even at 830 cm), and above 840 cm it is very loose and little humified. The bottom of the neighbouring pool is at about 770 cm (35 cm of mud, 165 cm of water near the boring, the depth decreasing northward). The bog development is thus in the direction of increasing wetness in a general but not entirely continuous way.

PROFILE ON RIVER BANK, UPSTREAM

Another profile from the same bog was obtained through excavation of a peat wall exposed by recent slumping of the river bank, the result of a local clay-slide about 600 m upstream from Transect I (650 m west of the preceding boring), and about 100 m downstream from the confluence of Muketei River (Plates VIII, *c*, and XXIV). River erosion in this place has carried away most of the wooded margin of the bog, and the exposed profile is located in the now drained transition between wooded and open bog. About one metre of peat was removed before samples were taken. Part of the profile was still frozen in July (*See* p. 114) but not in permafrost. This profile has been analysed by Terasmae (peat profile and pollen diagram, Fig. 5, in Terasmae and Hughes 1960).

Owing to repeated fires and to shrinkage due to the drainage caused by the river erosion, the thickness of the peat is only half of that of the profile in Transect I. The bottom level is at 644 cm above the late summer water-level of the river, which at this point may well be one foot or half a metre higher than at Transect I.

From the surface of the marine clay (or clayey till; small stones and gravel, mainly of limestone, occasionally present), brown clay and peat mixed with silty and clayey mineral matter extend only to 660 cm (4 feet 3 inches in the diagram). From 660 cm strongly decomposed peat with abundant woody roots extends to 683 cm, and with less abundant roots to 691 cm (3½ feet in the diagram). All these parts of the profile correspond well to the deposits from 597 to 707 cm in the Transect I profile, if the thicknesses measured in the latter are about halved. However, silt occurs fairly abundantly almost throughout the wood-peat (to 680 cm), which is rich in *Equisetum* spores (det. Terasmae). Most of the wooded stage thus represents a minerotrophic fen with trees, still within reach of occasional river floods.

A sample taken at 660 cm, in the lowermost peat belonging to the wooded fen, was analysed for C^{14} by the Groningen Laboratory, through the courtesy of the Geological Survey of Canada. The age of the sample is estimated at 4700±80 years (before the present). Unfortunately the elevation of the locality remains unknown. (The figure of 500 feet for the Missisa-Attawapiskat confluence downstream from our area is probably too high.) Potzger and Courtemanche (1954, 1956) reported a minimum age of 2350±200 years from near the bottom of a peat deposit at Smoky Hill Falls on the Rupert River, on the eastern side of James Bay; the elevation above sea-level there being only about 175 feet. According to Lee (1960), the highest coastal level is estimated at between 400 and 600 feet on the western side of the Tyrrell Sea (the ancient enlarged Hudson and James bays), and considerably higher on the eastern side. The maximum extension of this sea, contemporary with the ice-retreat from part of its area, occurred no less than 7,000 to 8,000 years ago, according to radiocarbon dating of marine shells (op. cit.), a method that now is suspected to give high results. In any case the radiocarbon dated peat sampled from the Attawapiskat river bank was probably formed a long time after the retreat of the Tyrrell Sea from this locality.

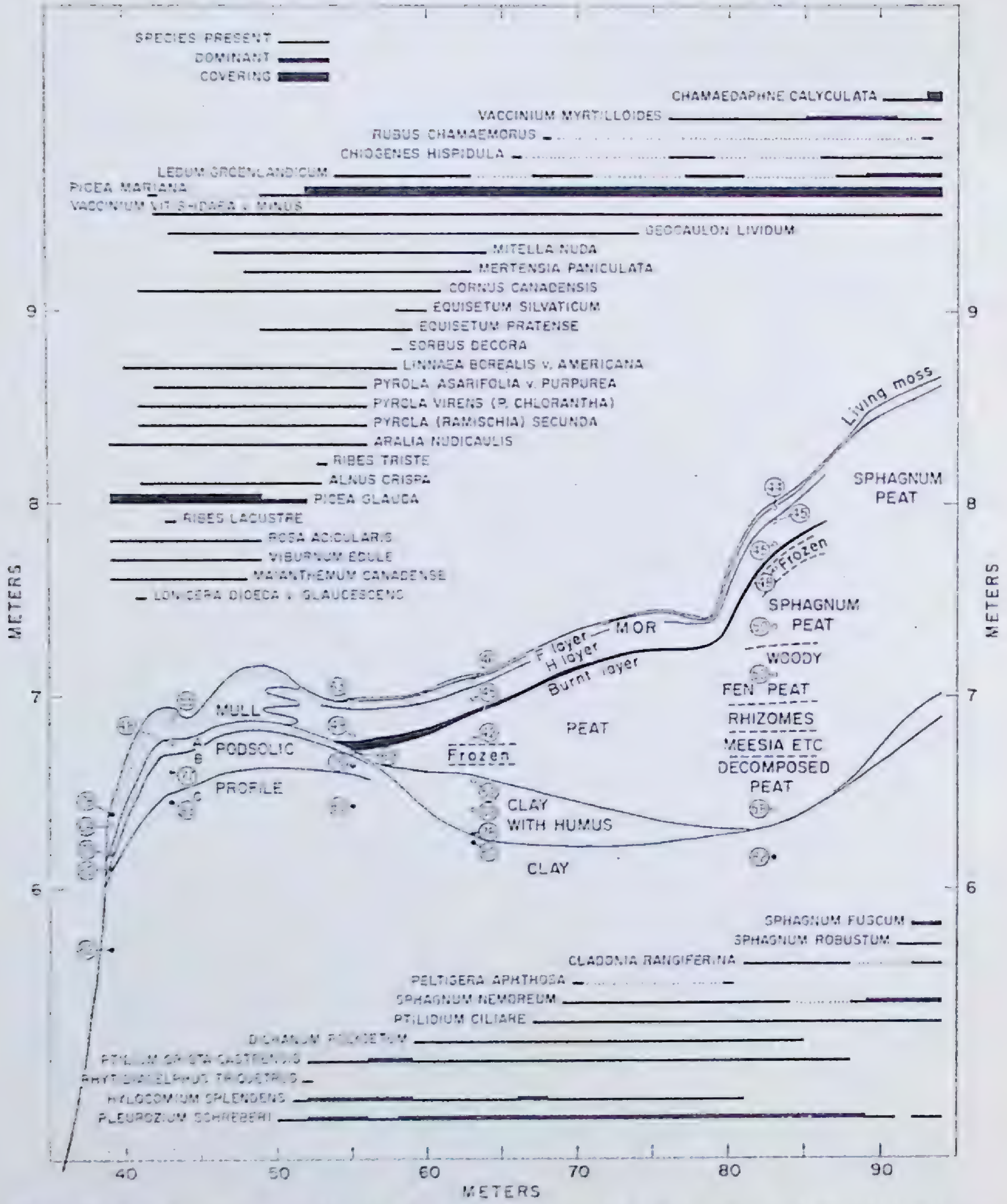
The upper metre of the river-bank profile consists of bog-peat, with a very variable degree of decomposition. Two strongly burnt horizons were noted.

SECTION ALONG TRANSECT II

Transect I cuts the marginal zone of the bog in an unusually low part, a little to the west of a small depression giving lateral drainage. The marginal part of the Transect bog and the adjacent river bank were therefore studied in Transect II, which is a little downstream from Transect I and shows a more typical marginal section. The bank at Transect II has normal height and is only moderately eroded on the riverward side; this erosion does not affect more than a part of the white spruce zone. We obtained a fairly complete "bisect" (i.e., transect also showing soil strata) through the white and black spruce zones, discontinued in the middle of the latter zone at 94 m measured from the low water shoreline. In this connection only the peat stratification in the bogward part need be mentioned. Fairly dense black spruce covers this part; the under-vegetation here shows ombrotrophic conditions in 30 m of the transect (beyond 64 m) where the bog surface rises 1.5 m, and the depth of the peat, which was still partially frozen in late July, increases from 0.5 to 1.8 m.

The peat deposit rests on marine clay which forms a shallow depression within the transected part of the black spruce bog zone, with its lowest part about 80 m from the river. This local little depression (the depth of which was only slightly more than 0.5 m) has had an early history different from the more normal development studied in the two profiles mentioned above. On the bottom of the depression (at 83 m in the Transect) a highly humified fen (or salt marsh) peat was deposited in water. Subsequently, near the presumed ancient water-level of the depression, i.e., about 50 cm above its bottom and 680 cm above the present low water-level of the river (which is here less than one foot lower than at Transect I), a remarkably well-preserved bryophyte carpet developed. In it, Dr. H. Persson (*see* Persson and Sjörs, 1960, p. 261) has identified the two species, *Drepanocladus tundrae* and *Meesia tristicha*, both minerotrophic and even calcicline, showing that the site was at that time a wet rich fen. The former species is an excellent climatic indicator of subarctic or arctic conditions. We found it growing at Winisk, but not in the Attawapiskat area, even though its present occurrence there is by no means unlikely. Its presence indicates a similar or slightly cooler summer climate than the present one.

Above the bryophyte layer is about 15 cm of peat, largely composed of coarse rhizomes of cyperaceous plants and *Equisetum fluviatile*. A great



Text Figure 7. Transect II (at the camp), across forested zone and wooded margin of bog; riparian part excluded. Ringed: pH values

number of roots from these penetrated down through the bryophyte layer. Later on, first the cyperaceous plants and then *Equisetum* disappeared, and deciduous shrubs succeeded them. The shrub-fen peat is about 30 cm thick, reaching to the 725-cm level. This development is similar to the early development in the above-mentioned radiocarbon-dated peat profile from the upstream river bank (Terasmae and Hughes, op. cit.). If the development was not synchronous, the bryophyte and cyperaceous layers would most likely be somewhat younger, because they were formed after the cessation of severe flooding in this locality. The bryophyte layer was probably formed in a not very late part of the postglacial "warm period" (Q-3 or xero-thermic period). The presence of an indicator of cool climate such as *Drepanocladus tundrae* is not too surprising, when we consider that the site was still fairly close to the coast of the Tyrrell Sea.

The next 50 cm of the profile (725–775 cm) consists of bog peat with *Sphagnum* and ericoid shrubs, probably *Chamaedaphne*. The formation of peat in this site, as well as in the more riverward parts of Transect II, was stopped by a severe fire. Above the burnt layer, no more true peat was formed. Instead, a forest humus of the mor type was deposited; this humus layer shows a very thick (17 cm) lower (H) horizon and a normal upper (F) horizon (6 cm). With 2 cm of living moss added, the present surface thus stands at 800 cm.

On the bogward side of the depression in the clay floor, the whole profile, except the lowermost 15 cm (i.e., 685–700 cm), consists of peat (165 cm at 93 m in Transect II) which was not examined. The lowermost layer is the usual interchanging humus and mineral soil derived from the early flooding period. Despite its slightly higher level, it was evidently formed prior to the *Meesia-Drepanocladus* layer, for the latter was never silted by the river floods.

Determination of water extract pH was made with one volume of fresh peat diluted to two volumes with distilled water; the mixture was shaken repeatedly and filtered after two hours, and pH was determined by glass electrode in the filtrate. The pH values are shown in Transect II. Upwards, the gradual decrease is very regular except in the riverward sites where the surface layers contain bands of alkaline river silt deposited during recent high floods. The pH development shows that influence of recent floods is absent in the more bogward part of the Transect. The recent pH values of deeper layers are probably not identical with the original ones, for it seems likely that at least the bryophyte and cyperaceous strata were originally more alkaline than at present, the pH values becoming gradually lowered as a result of penetration of acid water from above.

In one of the pits, well-preserved *Larix* twigs were found about midway from bottom to surface. A more interesting find was made on the south bank of the river where a clay-side had exposed a section of peat. Two black spruce cones were found in the bottom peat, showing that this species was a very early invader.

REMARKS ON SUCCESSION

General Views

The development of peatland through the filling-in of shallow ponds and lakes is one of the classical examples of unidirectional plant succession. Termed the "hydrosere," it has even been regarded as a cornerstone in the lofty building, the "steeple" of which is the climatic mono-climax theory. However, the greater part of the peatland area of the world was in fact formed through successions of the opposite type, leading to the paludification of terrestrial or semi-terrestrial sites. Even the hydroseral successions present a number of obvious anomalies (Sjörs, 1955, p. 157).

Through the unidirectional hydrosere, terrestrial sites are formed from freshwater sites, but the resulting land habitat and vegetation will never be identical with soil and vegetation developed on mineral substrate. Moreover, the development of peat cannot continue indefinitely in any site. If the present non-glacial period continues long enough, growing peat deposits will ultimately reach a state of instability inducing either drought or bog-burst, depending on the type of topography and climate. In many cases the peats will be destroyed earlier by erosion, corrosive oxidation, or fire, thus never reaching a final state of maturity. In the main boreal and subarctic zones, many peat deposits will probably never increase much beyond their present thickness, because peat growth is already effectively checked, particularly by oxidation (p. 73).

The presence of pronounced peatland patterns in the Hudson Bay lowland and the wide ecological variety of the plant communities in the peatlands show that the development there is far from unidirectional.

As an alternative to unidirectional succession, cyclic succession can be mentioned. There is evidence of cyclic succession in many ombrotrophic bogs elsewhere (*see*, in particular, v. Post and Sernander, 1910; Osvald, 1923, 1930, 1937, 1949, 1954). Although the details of most successional schemes have been deduced more from the vertical extension of recent plant communities than from the succession of peat strata, the interchanging of hummock and hollow peat is a well-established fact in many bogs, and it is usually very easy to demonstrate the "regeneration" by digging up hummock peat from under a present hollow. But the general applicability of the regeneration phenomenon has never been demonstrated, not even for ombrotrophic bogs. Cyclic succession is probably absent in the "stagnation complexes" of certain ombrotrophic bogs (Osvald, 1923, p. 291; 1925, p. 56, etc.; 1949, p. 11, 54: "retrogression processes"). Ratcliffe and Walker (1958, p. 427) explicitly state that regeneration was absent in the past development of the Silver Flowe (S. W. Scotland). Lundqvist (1951*b*) has given very clear evidence that cyclic succession is absent or subordinate in the more northern of the ombrotrophic bogs in the central Swedish upland (partly the same district and even the same bogs as those described by Sjörs, 1948). Aario (1932) gave similar evidence for bogs in Finland (province Satakunta). The Attawapiskat area shows a regional similarity to the northern parts of the above-mentioned Swedish and Finnish districts, and there are hardly any reasons to assume cyclic development in the Attawapiskat River bogs except locally and occasionally.

Minerotrophic peatland (fen) does not show cyclic succession except in special or local cases.

An interesting type of more or less cyclic succession occurs in central Alaska, according to Drury (1956). Wet, unfrozen areas expand at the expense of elevated, permafrosted, wooded platforms which melt laterally, much in the same way as the "black spruce islands" described above (p. 107). According to Drury (l.c.) succession in the wet peat areas gives rise to hummocks which again become permanently frozen and elevated. Judging from Drury's aerial photographs, the former process is the more active one under the present climatic conditions. This type of cyclic succession does not occur in our area, where permafrost is only of local occurrence (in the "black spruce islands").

Being neither unidirectional nor cyclic in our area, the successions must then be multidirectional or seemingly irregular, i.e., governed by local conditions or by unpredictable events such as fire. A discussion of the importance of disturbance, including rare and unpredictable events, for plant succession in various climatic zones is given by Raup (1957). Through multidirectional or irregular successions, the landscape remains heterogeneous or may become increasingly diversified rather than develop toward uniformity. The successions in northern peatlands are manifold and lead to divergent and complex results that largely depend on local physical and chemical conditions.

In all regions where peatlands are truly extensive, particularly in cool oceanic regions and in the boreal and subarctic zones, the expanses of peatlands were largely formed by paludification of mineral soil, and only to a small extent by hydroseres starting in shallow water. That this must be so has long been known to paludologists (e.g., Malmström, 1923, 1931; v. Post and Granlund, 1926; v. Post, 1927; Granlund, 1932) but is too frequently overlooked by students of general succession. The successions that have led to peatland formation on terrestrial sites are naturally strongly divergent from those concerning the mineral soils that remained unpaludified. The sites of present peatland and those of forest were often rather similar originally, but for various reasons they developed different patterns of drainage. Those sites that became paludified were affected by increasingly impaired drainage, a cause, as well as an effect, of incipient peat accumulation. Other sites remained better drained and did not develop peat deposits. Both types of succession have occurred simultaneously, i.e., under identical sequences of climatic changes.

The physiographic conditions of the Hudson Bay Lowland evidently have led to a great dominance of the paludification type of succession, until almost no well-drained mineral soil remained. In the interior, this trend has continued longer than in the more youthful coast area.

PEATLAND SUCCESSIONS IN THE ATTAWAPISKAT RIVER AREA

The first types of vegetation to appear on the rising, low, clayey western shores of the Tyrrell Sea (Lee, 1960) were intertidal salt marshes. Owing to the initial rapid rate of the land rise, no beach ridges or dunes seem to have been formed in what is at present the more elevated interior of the lowland, although low ridges may have been buried completely by the peat cover. The subsequent uplift was greatest in the east (*see*, e.g., Lee, 1960), and therefore the original gradient must have been somewhat greater than now, resulting in slightly better drainage. The newly exposed land was invaded by forest soon after its emergence. Much of this early forest probably was swampy, however, and formed peaty but well-decomposed types of humus, which made the soil less permeable and more water-retaining. The general development thus was in the direction of greater wetness, and very gradually the swampy forests became first wooded fens and then open fens or bogs.

Local wet depressions seem to play an important part as early centres in the paludification process. Along streams such waterlogged areas were continuously formed through various processes. In some less elevated parts of the lowland, particularly at moderate distance from the Hudson Bay coast, small streams follow a zig-zag course owing not to true meandering but to numerous ancient beach ridges at right angles to the general slope (Hustich, 1957*b*, Fig. 1). Between such beach ridges paludification probably began directly without a swamp forest stage. The topography of the middle Attawapiskat River area lacks features of this kind. The formation of true meanders is common in certain other parts of the lowland (Hustich, op. cit., Fig. 2) and leads to slower flow of the streams and to a higher water-level in their surroundings. Only a few streams are meandering near the Muketei-Attawapiskat confluence, but some good examples occur farther south. The general, but unequal, land uplift also caused most streams to become slower. The smallest streams were choked up to some degree by peat-forming vegetation.

A major contributing factor in the paludification of the boreal forest zone is the beaver (David Thompson: Tyrrell 1961; observations by Porsild; Sjörs, 1959, p. 16). Owing to the general flatness of the Hudson Bay Lowland, beaver ponds (Plate XXV; Hanson and Smith, 1950, fig. 57, p. 138) here tend to become very extensive, causing large-scale flooding and consequent "drowning" of forested land. These changes seem to be intermittent rather than continuous. Possibly the present increase in the beaver

PLATE XXV

A beaver pond just west of Muketei River. Local paludification of spruce forest
—*Photo G. Sjörs*

population, following a long period of low numbers because of overexploitation, is responsible for this impression. Before the fur trade had created a market for beaver pelts, the beaver population in many parts of Canada must have been very large and its effect on the Canadian landscape much greater than at present. In the Hudson Bay Lowland, in the early post-marine stage, before the rivers had eroded down to their present boulder beds, swampy forests and large areas of seasonally flooded land could provide food for innumerable beavers.

The development of extensive ombrotrophic areas (bogs) in the originally minerotrophic peatland (fen) has taken place later than the general paludification, but some ombrotrophic areas may have developed directly from forest, the forest humus (mor) becoming very deep and thus gradually changing into accumulative peat. Occasional fires counteracted this development.

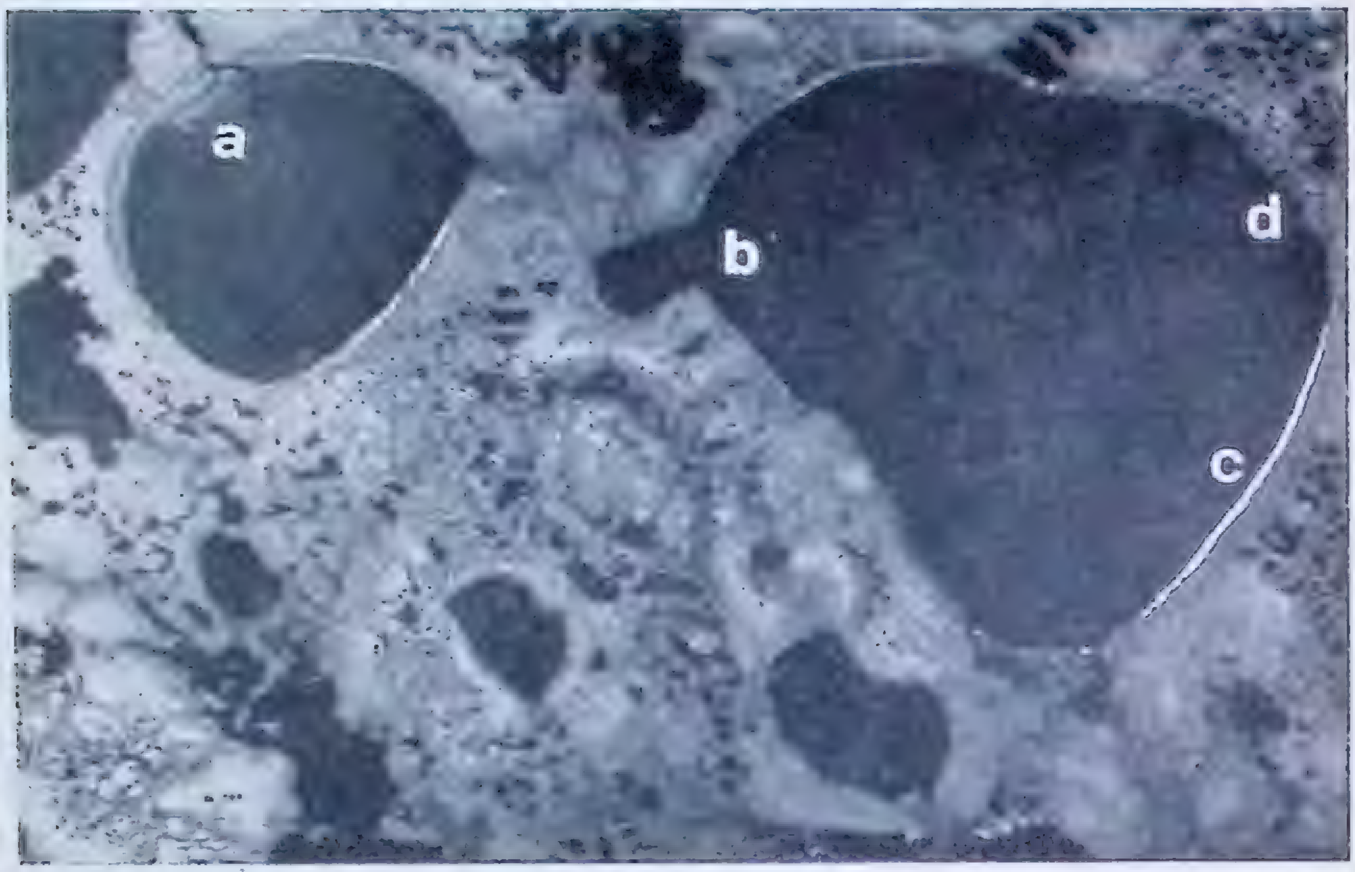
Later events in the history of the peatlands were the formation of bog-hollows and bog-pools in the ombrotrophic areas and the formation of "flarks" in the parts remaining minerotrophic. This process of pattern formation was probably contemporaneous with, or preceded by, the deterioration of climate, which is known to have occurred gradually or intermittently and to have been completed in Europe about 2,500 years ago. There is evidence for a similar more or less contemporaneous climatic change in Canada, as shown by pollen diagrams and archaeological studies. Also the age of the permanently frozen "black spruce islands" may be about the same. However, no direct evidence of the age of these patterns and structures is as yet available.

During the last 2,000 years or so, the changes seem to have been comparatively small, except near the coast, where the uplift and paludification is still going on, although at a slower rate than in the early post-glacial period. Paludification at present seems to involve a direct change of coastal salt marshes into peatland (Moir, 1954), even though some of the zonations described by Ritchie (1957, 1960*c*) may involve succession by way of intermediate forested stages particularly near rivers. In the interior, the growth of the peat deposits accentuated their hydrotopography, the distinction between different types becoming more marked. Occasional fires undoubtedly resulted in temporary or permanent changes in some of the drier sites. Pools and flarks grew deeper, but many of the "black spruce islands" collapsed, partly, or fully, through melting of their ice cores, partly as a result of insolation, following local fires, but also as a consequence of the recent amelioration of the climatic conditions.

THE ORIGIN OF LAKES

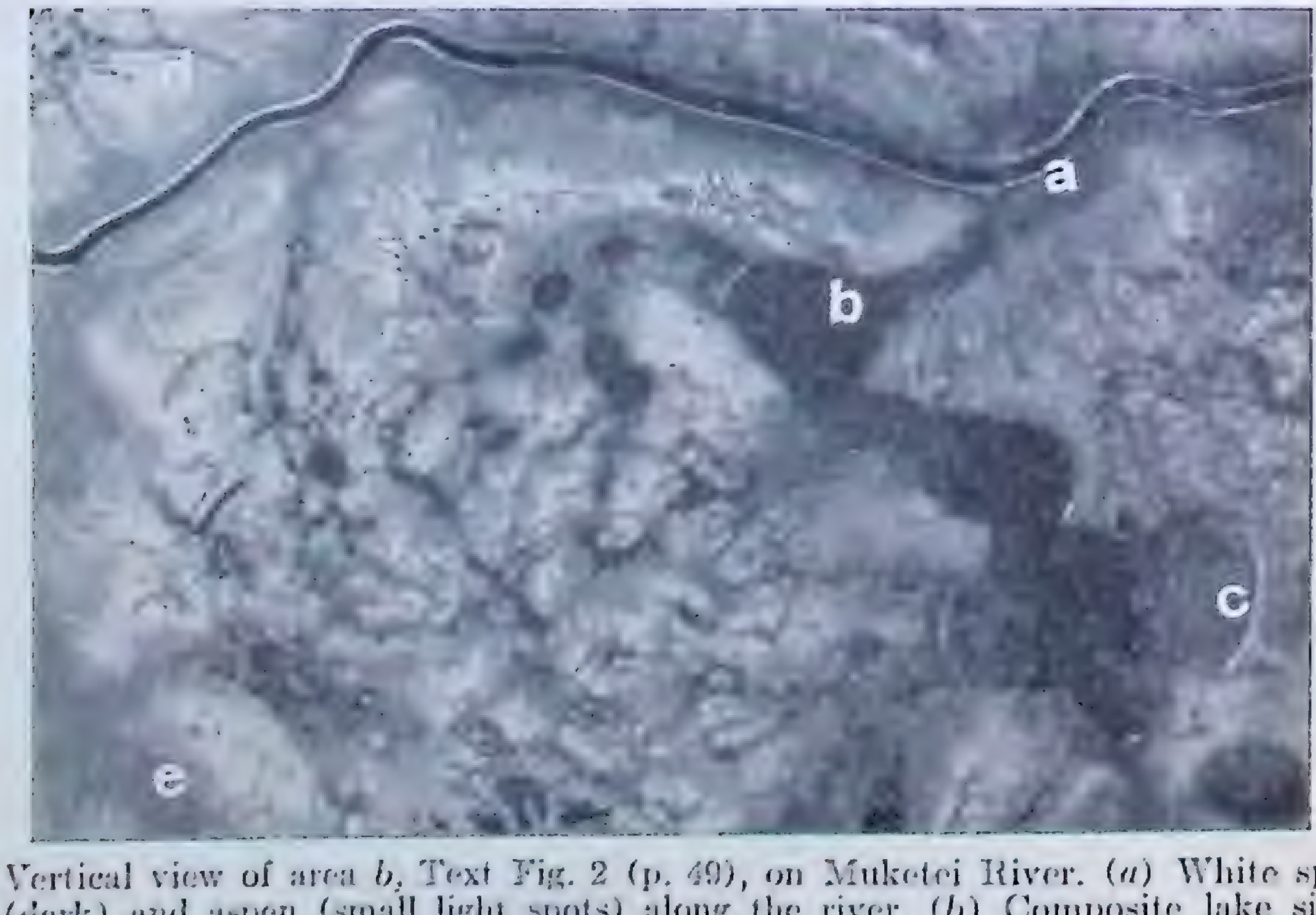
A special problem is the origin of the numerous roundish lakes in some parts of the peat-covered lowland. Although Hanson and Smith (1950, pp. 92, 100, etc.) expressed opinions to the contrary, the appearance of such lakes does not indicate, except locally, that they are in the process of being filled in by vegetation, with subsequent formation of peatland. Their shores even show abundant evidence of peat erosion, presumably through the combined effects of wave action and corrosive oxidation in summer

PLATE XXVI



A. Vertical view of area *a*, Text Fig. 2 (p. 49), north of Muketei River. (*a*) Round lake showing bottom deposits west of the outlet from the top left lake, indicating clockwise rotation of lake water. (*b*) Small lake having joined the larger one. (*c*) Lake erosion cutting into the pool pattern of a raised ombrotrophic bog

—*Photo by R.C.A.F.*



B. Vertical view of area *b*, Text Fig. 2 (p. 49), on Muketei River. (*a*) White spruce (dark) and aspen (small light spots) along the river. (*b*) Composite lake site of Pl. XXVII). (*c*) Mineral beach. (*d*) Ombrotrophic bog with two seepages. (*e*) Black spruce islands along meandering brook

—*Photo by R.C.A.F.*

and ice pressure in winter. Along certain lake shores the mineral substrate is also affected, resulting in light-coloured crescent-shaped beaches easily identified on aerial photographs. Seen from the air, the lake bottoms in the Attawapiskat area are always dark, in contrast to the white bottoms of shallow lakes in the highly calcareous Sutton Ridge area (*see* Sjörs, 1961 *b*). The dark colour may be due to strong humic discoloration of the water, but more likely in this area to mud or peat bottoms.

There seem to be ample reasons for believing that many of the lakes seen by us or studied on air photographs are actually becoming larger. An example is given in Plate VI B. In another case (Plate XXVI B) near the Muketei River, several (probably six) roundish lakes appeared to have coalesced as a result of erosion. This composite lake showed both mineral beaches (*c*) and eroded peat shores (*b*). The former were not visited; the aquatic vegetation along the latter was scanty (*Myriophyllum exalbescens, Potamogeton Richardsonii*). The water-level seemed to have risen (Plate XXVII), and we found remains of a beaver dam in the small stream flowing from the lake.

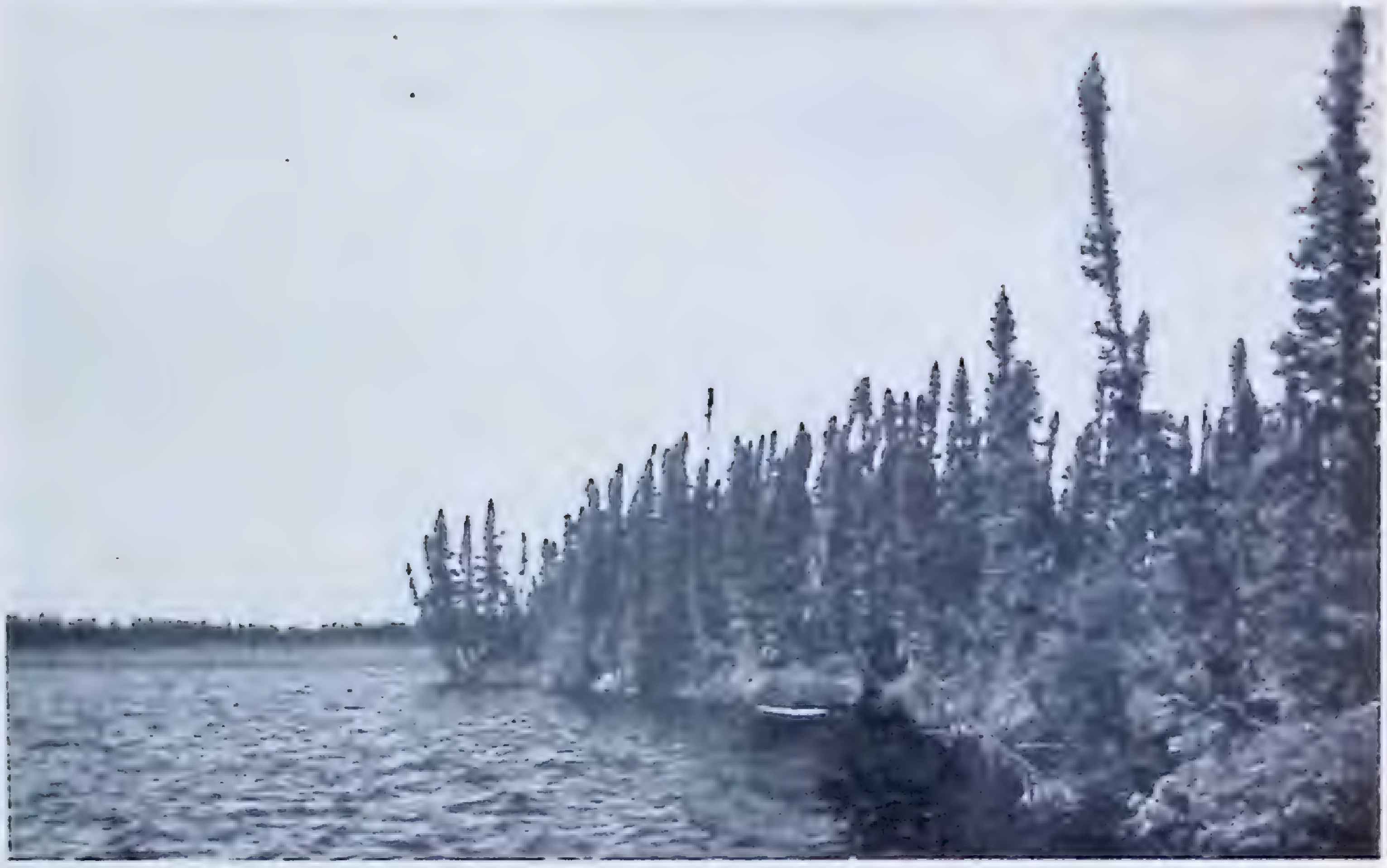
In a small lake east of the "transect bog" a beaver dam had caused a very recent rise in the water-level, which was considerably noticeable in a brook 500 metres upstream from the lake, and even noticeable nearly one mile upstream. Numerous other instances of expanding beaver ponds were observed from the air.

It even seems possible that the majority of small- and medium-sized lakes in the lowland are not at all primary bodies of water. Lakes are very rare near the present coast, and frequent only in certain older parts of the lowland flats (cf. Hanson and Smith, 1950, pp. 96–101). It is possible but not very likely that depressions (later being occupied by lakes) were particularly common in those shallow parts of the Tyrrell Sea that emerged between the major rivers during the early phase of land uplift (op. cit., p. 97). The distribution of lakes would be easier to explain if they were interpreted as secondary formations in flat areas of sufficient age. They may have developed from beaver ponds in small watercourses and from coalescent pools in the fens and, to a smaller extent, in the bogs. Such initial stages may have been expanded further by the effects of still higher beaver dams and through ice pressure, wave erosion, and corrosive oxidation of peat surfaces. The watershed areas have developed a multitude of such presumably secondary lakes, probably because the lack of a gradient made drainage so poor from the beginning that lakes were formed early and easily.

POTENTIAL RESOURCES OF THE AREA

The small Indian villages in the Hudson Bay area have become in modern times increasingly dependent on supplies from outside, even of food, because food resources are not fully utilized in their own territories. Agriculture, raising of livestock, and lumbering are practically non-existent except very locally but would almost certainly be practicable, at least in the southern and interior parts, on a moderate scale sufficient for local use. Even with due regard to the extraordinarily small extent of mineral

PLATE XXVII



Wave-eroded wooded margin of lake. The high water-level is maintained by a beaver dam across the outlet. Leaning, but up-curved, black spruce trees show that erosion, although active, is very slow. Just south of Muketei River (point *b* on Pl. XXVIIB)

soils, any similar area in the Old World would sustain and even feed a population several times larger. One reason why natural resources are not developed is that practically the entire population lives in summer near the coast of Hudson and James bays where the summer climate is much less favourable than that of the interior.

Although further analytical data and considerable experimental work are needed before the present investigations can be considered useful for economic purposes, general experience from forestry and agriculture in comparable northern peatland districts can be applied to some extent after basic knowledge of the natural habitat and vegetation is available. Of the types of peat areas described in the present paper, only the already wooded, minerotrophic peatland would respond to drainage by reasonably improved forest growth. Despite the small general gradient in the lowland, certain parts of the peatland areas would not be difficult to drain. In draining minerotrophic peatlands, not only must the peat area itself be drained, but also the affluents must be cut off by ditches.

Drainage alone would not be sufficient for agricultural needs and should be followed by heavy applications of phosphorus and probably potassium also. Shallow minerotrophic peat areas, burnt to a depth sufficient to permit subsequent mixing with some of the mineral subsoil, would be best for agriculture; deeper minerotrophic peat deposits could be cultivated, provided the drainage can also be made efficient after the considerable shrinkage of the peat which would result. Very wet minerotrophic sites and all ombrotrophic sites are unfit for this purpose.

The best potentially arable soils, however, are found on high but narrow mineral terraces along the rivers, at present occupied by aspen or white spruce. Mineral soils usually need nitrogen fertilization, but deficiency in phosphorus and possibly potassium can also be expected in some cases. Any permanent settlement on river-bank sites should be at least 30 feet above the river, because of the danger of severe spring floods caused by occasional ice-jams. The excellent alluvial soils on lower parts of the banks and islands could be used to good advantage for grazing and for hay crops, which are also the most suitable crops for drained peats. Cattle raising for local needs of milk and meat is by far the most important form of agriculture in those northern peatland districts that sustain a rural population (particularly in Finland).

Winter wheat and oats would probably ripen only on well-drained mineral soil in the extreme south and southwest of the Hudson Bay Lowland. On the other hand, there is little doubt that barley, winter rye, potatoes, and some vegetables (perhaps started under glass) could be grown in large parts of the interior. Potatoes and a few hardy vegetables have been grown successfully even at the settlements near James Bay (Moose Factory, Albany, and Attawapiskat; Dutilly, Lepage, and Duman, 1954, p. 4), and there is a small vegetable garden at the St. Anne Catholic Mission near Fort Albany. Vegetables important to the diet of the Indian inhabitants could certainly be produced much more successfully in the interior. The importance of selecting sites with favourable soil and local climate is well known from outposts of potato cultivation in the northern uplands of Scandinavia.

Nevertheless, even though the better parts of the lowland offer potential possibilities for agriculture and forestry on a small scale, this area is much less favourable than are many other as yet unsettled districts in central and even northwestern Canada. Most of the possibilities for productive development will probably long remain unexploited, but the use of some of the resources could well benefit the small local population, whose economy is on a very unsatisfactory basis since the decline of the fur trade, on which it was formerly entirely dependent.

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DISTRIBUTION OF DWARF MISTLETOES AND THEIR FUNGUS HYPERPARASITES IN WESTERN CANADA

By Job Kuijt

There are certain patterns in the distribution of dwarf mistletoes that merit presentation and documentation. Western Canada was not, of course, considered in Gill's monograph (1935), except for some casual remarks. In 1960 an account of the distribution of dwarf mistletoes in California was published (Kuijt, 1960*b*), where three species reach their southward limits. In the Canadian West these same species reach their northern extent, as will be seen below.

Taxonomically, the only points of controversy lie perhaps within *Arceuthobium campylopodum*, in our area known as hemlock mistletoe or

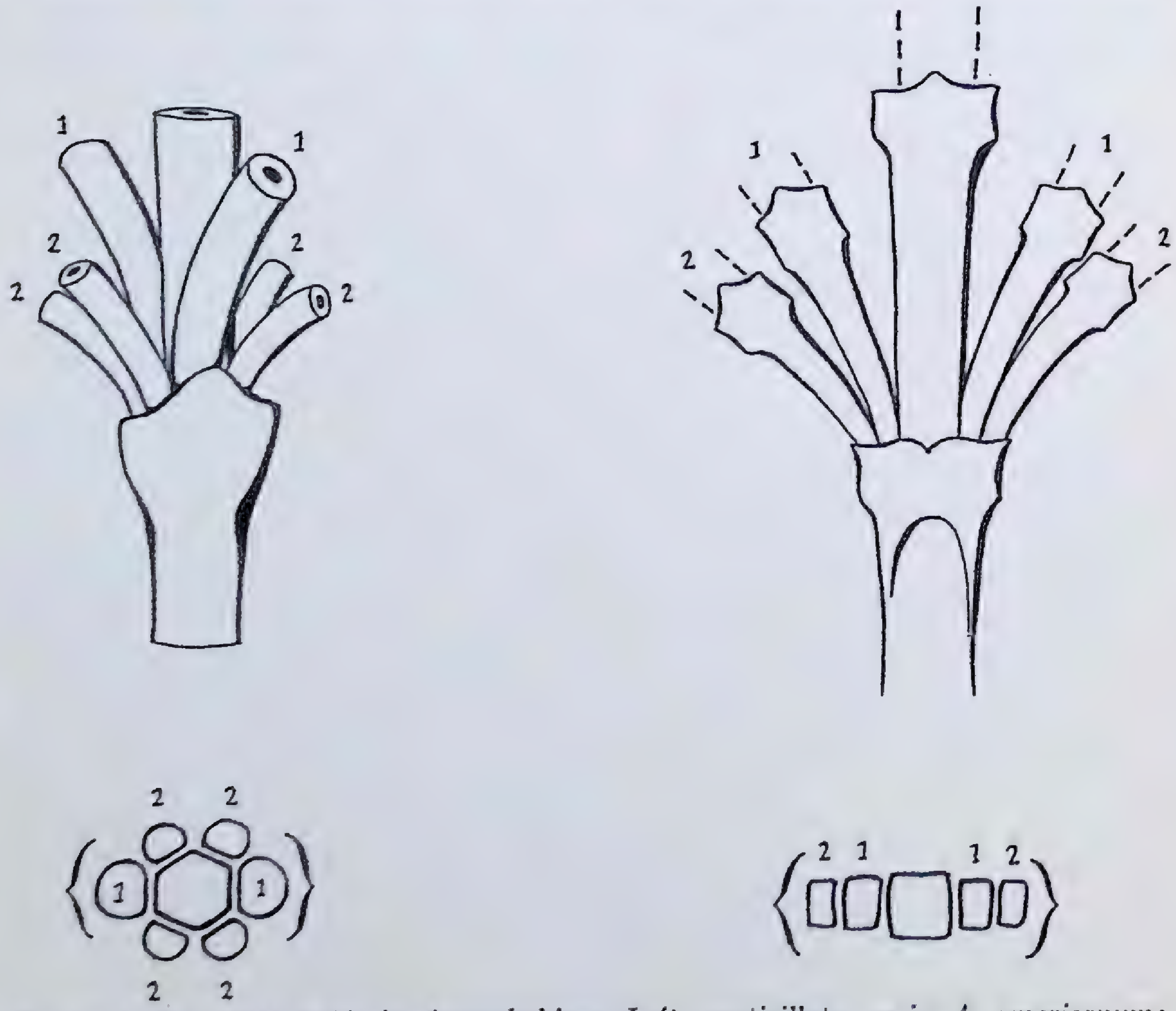

Figure 1. Branching habit in *Arceuthobium*. *Left*: verticillate, as in *A. americanum*; *right*: fan-like, as in *A. campylopodum*

larch mistletoe. I have commented on the use of infraspecific categories in *A. campylopodum* elsewhere (Kuijt, 1960*a* and *b*), and there is no need for repetition here. At this time it does not seem desirable to employ any subdivisions of this species, although some sort of acceptable subspecific organization may eventually be worked out. Gill's categories, based on host preferences only, are unsatisfactory. The sporadic natural transfers in our area of *A. campylopodum* from *Larix* and *Tsuga* to *Abies* and *Picea,* for example, demonstrate the unsatisfactory delimitation of *A. campylopodum* f. *laricis,* f. *tsugensis,* f. *abietinum,* and so forth, as taxonomic categories.

The frequency of misidentified specimens prompts me to include keys to aid those persons charged with identification of specimens. These keys are designed to apply only to the four species reported from the area here considered. In this connection the reader should be warned against the use of pistillate flowers as a guide to flowering time, as those of fall-flowering species change little or not at all until the following spring. I am including (in an auxiliary way only) some key characters based on known host preferences.

The specimens cited in this paper represent only a part of the collections seen. As pointed out previously (Kuijt, 1960*a*), the citation of all specimens would result in a false impression of local frequency. Locations such as Banff, Alta., and Victoria Beach, Man., are represented in herbaria in numbers of collections quite out of proportion with the relative abundance of mistletoe.

I wish to express my appreciation for the assistance rendered by the various curators of herbaria referred to in the text. My thanks go to Dr. T. M. C. Taylor for reading the manuscript.

KEY TO *ARCEUTHOBIUM* SPECIES IN WESTERN CANADA

1. Flowers present (use staminate flowers only).................	2
1. Flowers absent, or only pistillate ones available.................	5
2. Flowers in spring or early summer; staminate flowers often pedicellate...	3
2. Flowers in late summer or fall; staminate flowers sessile in the axils of scale leaves...	*A. campylopodum*
3. On *Pseudotsuga*, very rarely on *Abies*...........................	*A. douglasii*
3. Not so...	4
4. A rather large, slender, yellowish to olive green, branched mistletoe, usually on *Pinus*, rarely on *Picea glauca*. Branching habit and inflorescence verticillate: usually 6 branches or flowers at one node in a whorled fashion (*see* Fig. 1).............................	*A. americanum*
4. Plants smaller than 35 mm, often somewhat purple, very sparsely branched, branches no more than 2 at one node. Almost invariably on spruce; not known from Alberta or British Columbia..........	*A. pusillum*
5. Plants larger than 35 mm, often profusely branched.............	6
5. Plants smaller than 35 mm, sparsely branched or unbranched.....	7
6. Branching verticillate: usually 6 branches or flowers at a node in a whorled fashion (*see* Fig. 1). Not known from *Abies*, *Larix*, *Pseudotsuga* or *Tsuga*, and not found west of the Coast Range...	*A. americanum*

6. Branching fan-like; all lateral branches of one node arranged in one plane, the shortest laterals below (*see* Fig. 1). Not known from *Pseudotsuga*, and not found east of the Rocky Mountain Trench . . *A. campylopodum*

7. Predominantly on *Pseudotsuga*, and only in the southern interior of British Columbia . . . . *A. douglasii*

7. Predominantly on *Picea*, and not known from Alberta or British Columbia . . . . *A. pusillum*

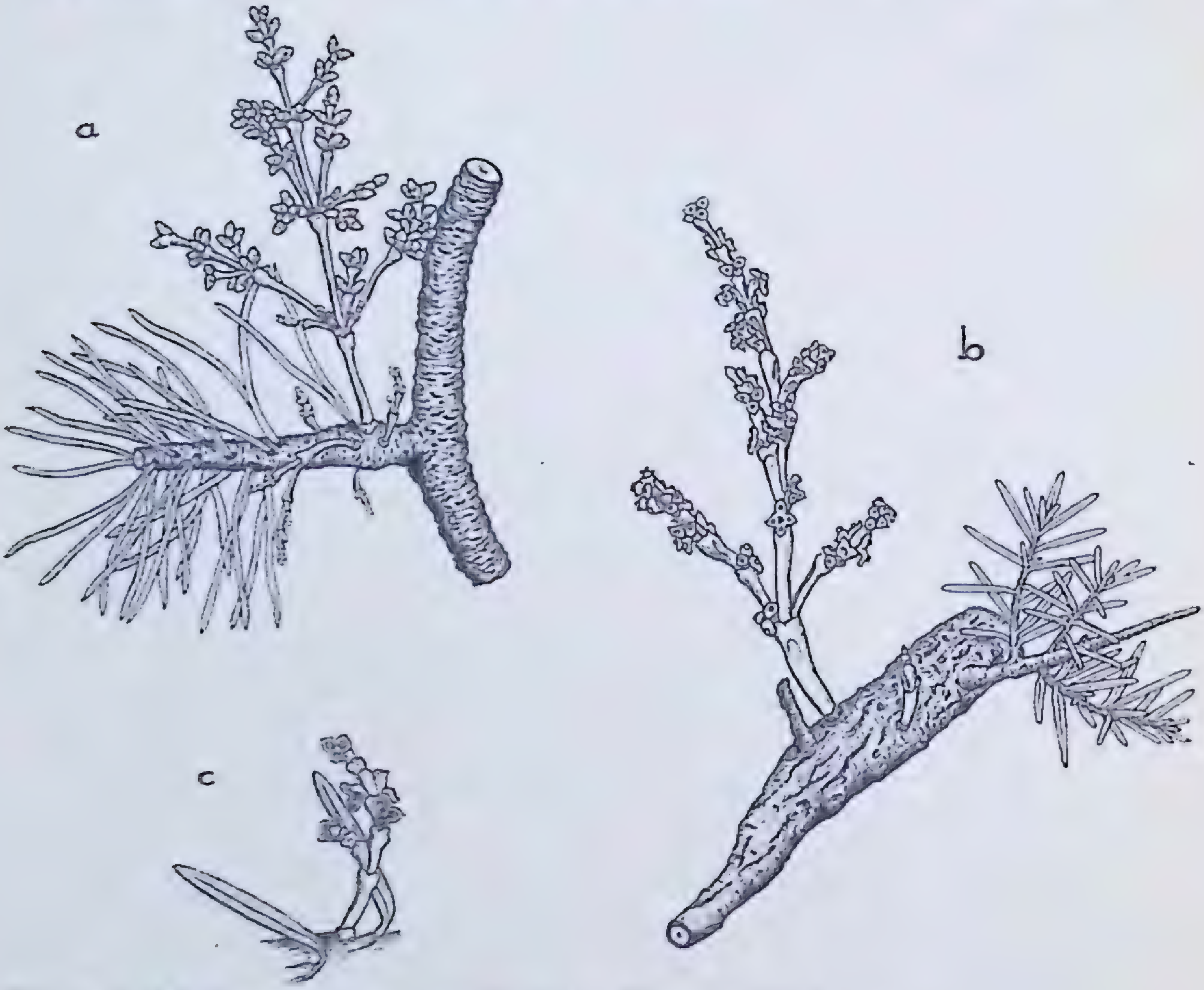

FIGURE 2. (a) *A. americanum*, pistillate, on *Pinus contorta*
(b) *A. campylopodum*, staminate, on *Tsuga heterophylla*
(c) *A. douglasii*, staminate, on *Pseudotsuga menziesii*
All figures natural size

A. americanum Nuttall ex Engelmann

Lodgepole pine mistletoe, jack pine mistletoe. Figure 2a.

Specimens Seen: (the hosts, *Pinus banksiana*, *P. contorta*, *P. ponderosa*, and *Picea glauca* are indicated by Pb, Pc, Pp, Pg, respectively)

MANITOBA: Bisby, Victoria Beach (WIN*), Pb; Gillett & Scoggan 10118, 35 mi. south of The Pas (DAO), Pb; Jackson, Mile 62, Grand Beach (WIN), Pb; *idem*, Grand Rapids (WIN), Pb.

*Abbreviations used to indicate the herbaria in which specimens are deposited are the standard ones recommended by "Index Herbariorum, Ed. 4."

Saskatchewan: Breitung 8366, Beauval, 150 mi. north of Meadow Lake (DAO), Pb; *idem* 8430, Waterhen Forest Reserve, 50 mi. north of Meadow Lake (DAO), Pb; Dore 47, Fort à la Corne Reserve (DAO), Pb; Fraser, Prince Albert (DAO, SASK), Pb; Glen, Emma Lake (UBC), Pb; Russell 4754, Lac La Ronge (DAO), Pb; Whitney & Chamberlain, Torch River, Candle Lake (UBC), Pb.

Alberta: Baranyay, 50 mi. southwest of Nordegg (CFB), Pc; *idem*, Keywood Cabin, Mercoal-Hinton road (CFB), Pc; Black, Saskatchewan River Crossing, Banff Nat. Pk. (CFB), Pc; Bourchier, Sunwapta Falls, Jasper National Park (CFB), Pc; *idem*, Herbert Lake, Banff National Park (CFB), Pc; *idem*, 3 mi. north of Bow Summit, Banff-Jasper road (CFB), Pc; *idem*, Coronado (CFB), Pb; *idem*, Smoky Lake (CFB), Pb; *idem*, Bellis (CFB), Pb; *idem*, Perryvale (CFB), Pb; Bourchier & Stevenson, Kananaskis Forest Expt. Sta. (CFB), Pg; Breitung 5586, west of Spring Creek Ranger Station, Cypress Hills (DAO), Pc; Brown 794, Bankhead, 4,500 ft. (CAN), Pc; Dempster, Jasper (CFB), Pc; Kuijt 512, Whitecourt (CFB), Pb; *idem* 530, Nestow (CFB, UBC), Pb; *idem* 531, Calling Lake (CFB, UBC), Pb; *idem* 532, Smith (CFB, UBC), Pb; *idem* 539, Mi. 40, Coleman road south of Seebe (CFB), Pc; *idem* 541, Grand Trunk road, Red Deer River crossing (CFB), Pc; LaRue, Athabasca (CFB), Pb; Loman & Wilkinson, Owl River, 23 mi. north of Lac La Biche (CFB), Pb; McCalla 11844, 11845, sandhills about 14 mi. north of Fort Saskatchewan (UBC), Pb; McNeil, 6 mi. south of Hondo (CFB), Pb; Moss 4769, river flats, Jasper (ALTA), Pc; *idem* 8141, sandhills southwest of Grande Prairie (ALTA, DAO), Pc; *idem* 8698, 8699, St. Vincent, north of St. Paul (DAO, ALTA, respectively), Pb; *idem* 9504, sandhill area northeast of Bruderheim (ALTA), Pb; Patterson, 17 mi. northeast of Fort Assiniboine (CFB), Pb; Paul & Blauel, Whitecourt (CFB), Pb; Raup & Abbe 4449, Shelter Point, north shore of Lake Athabasca, 700 ft. (CAN, NY), "Pc"; *idem* 4472, Sand Point, north shore of Lake Athabasca (CAN, NY), "Pc"; Spreadborough 20231, Maligne and Athabasca rivers, Jasper National Park (CAN), Pc; Stanley, 8 mi. south of Grande Prairie (CFB), Pb; Thornton & Bourchier, 8 mi. north of Clearwater River (CFB), Pc; Watson, Spray River Valley, Banff National Park (CFB), Pg; Wilkinson, 14 mi. northwest of Philomena (CFB), Pb; *idem*, 7 mi. west of Cold Lake (CFB), Pb; Williamson, Upper Hot Springs road, Sulphur Mt., Banff National Park (DAO), Pc; Wilson, Wood Buffalo National Park, 59° 09′ N, 112° 25′ W (CFB), Pb (the most northerly collection known from the *Loranthaceae*).

British Columbia: Bourchier, Vermilion Crossing, Kootenay National Park (CFB), Pc; Bourchier & Kuijt, Mi. 9, Settler's Road, Kootenay National Park (CFB), Pc; Brayshaw 48132, west of Peachland, 3,000 ft. (UBC), Pc; Brink, Bonaparte River near Cache Creek (UBC), Pc; Brooks 5, near fish trap bridge of Anahim Lake (UBC), Pc; Calder, Parmelee & Taylor 16644, *ca.* 10 mi. north of Clinton (DAO), Pc; *idem* 17730, base of Mt. Bowman near Jesmond (DAO), Pc; *idem* 19159, Kleena Kleene P.O. on One-Eye Lake (DAO), Pc; *idem* 19231, 4.1 mi. west of Kleena Kleene P.O. on road to Anahim Lake (DAO), Pc; Calder & Savile 11974, Kinbasket River delta, northeast side of Kinbasket Lake (DAO, UBC), Pc; *idem* 12108, northeast slope of Mt. Carnarvon, Yoho River valley (DAO), Pc; Calder, Savile & Ferguson 13896, 3 mi. north of Sinkut Mt., 10 mi. south of Vanderhoof (DAO, UBC, V), Pc; *idem* 13942, 1 mi. north of Heart Lake, 45 mi. north of Prince George along Hart Highway (DAO, UBC), Pc; *idem* 14363, outskirts of Prince George (DAO, UBC, WTU), Pc; *idem* 15273, 2.5 mi. southwest of Telkwa (DAO, UBC), Pc; *idem* 15350, Meier's Lodge at northwest end of Cluculz Lake (DAO, UBC), Pc; Cornwall 1562, near Ashcroft (DAO), Pc; Dawson 23782, Guichon Creek (CAN), Pc; *idem* 23785, Elk River, Kootanie Valley (CAN), Pc; *idem* 23786, between Similkameen and Nicola (CAN), Pc; Duerksen, Beaverdell (DAVFP), Pc; *idem*, Kitchener (DAVFP), Pc; Farr, Emerald Lake (BM, K), Pc; Hitchcock & Martin 7425, near Guichon Creek, *ca.* 13 mi. south of Savona (DS, NY, WTU), Pc; Kuijt 527a, Kimberley (CFB, UBC), Pc; *idem*, 8 mi. north of Kimberley (CFB), Pp; *idem* 528, Windermere (CFB, UBC), Pc; *idem* 535, Yellowhead (CFB), Pc; *idem* 536, Fraser River crossing west of Yellowhead Pass (CFB, UBC), Pc; *idem* 557, Anarchist Mt. (CFB), Pc; *idem* 564, Nakusp (CFB), Pc; *idem* 567, Moyie Lake (CFB, UBC), Pc; *idem* 568, Bull River (CFB, UBC), Pc; *idem* 569, Kinbasket River (CFB, UBC), Pc; *idem* 570, 571, Sunday Summit (CFB, UBC), Pc; *idem* 572, 574, between Balfour and Nelson (CFB, UBC), Pc; *idem* 575, 578, Balfour (CFB, UBC), Pc; *idem* 582, 10 mi. north of Sunday Summit (CFB, UBC), Pc; *idem* 2385, banks of S. Thompson River 5 mi. west of Chase (UBC), Pc & Pp; Landells, Golden (UBC), Pc; Morris, Summit Lake, Mi. 38, Hart Highway (DAVFP), Pc; Shelford, Wistaria (V), Pc; Sugden, Aspen Grove (DAVFP), Pc; Sullivan 571, 20 mi. south of 100 Mile House (V), Pc; Taylor 1300, Cathedral Lakes, Ashnola District, 5,000 ft. (UBC), Pc; Taylor & Lewis 426, Ootsa Lake (UBC, WIN), Pc; Thomas, Merritt (DAVFP), Pc; *idem*, Davie Lake, Prince George (DAVFP), Pc; *idem* 19, Grand Forks (DAVFP), Pc.

Discussion

The Victoria Beach locality, already known at the time of Dowding's work (1931), is the most easterly locality from which specimens have been seen in the course of this study. Hord & Quirke (1956), however, have recorded *A. americanum* on *Pinus banksiana* from White Otter Lake, Kenora District, Ontario. From there the parasite follows the jack-pine belt to central Alberta, and thence south and southwest along the mountains. The Athabasca Lake and Wood Buffalo Park stations represent the most northerly localities not only in the genus, but probably also in the entire family. Further to the west, the lodgepole pine mistletoe is virtually unknown from the northern half of British Columbia. Future collectors will, in all probability, extend the known range of this species in this direction, although the northernmost limit of the host has almost certainly not been reached by the mistletoe.

Attention should be drawn to the very extensive map in Zalasky (1955) of the distribution of *A. americanum* and *A. pusillum* in Saskatchewan and Manitoba. Unfortunately, the specimens upon which this

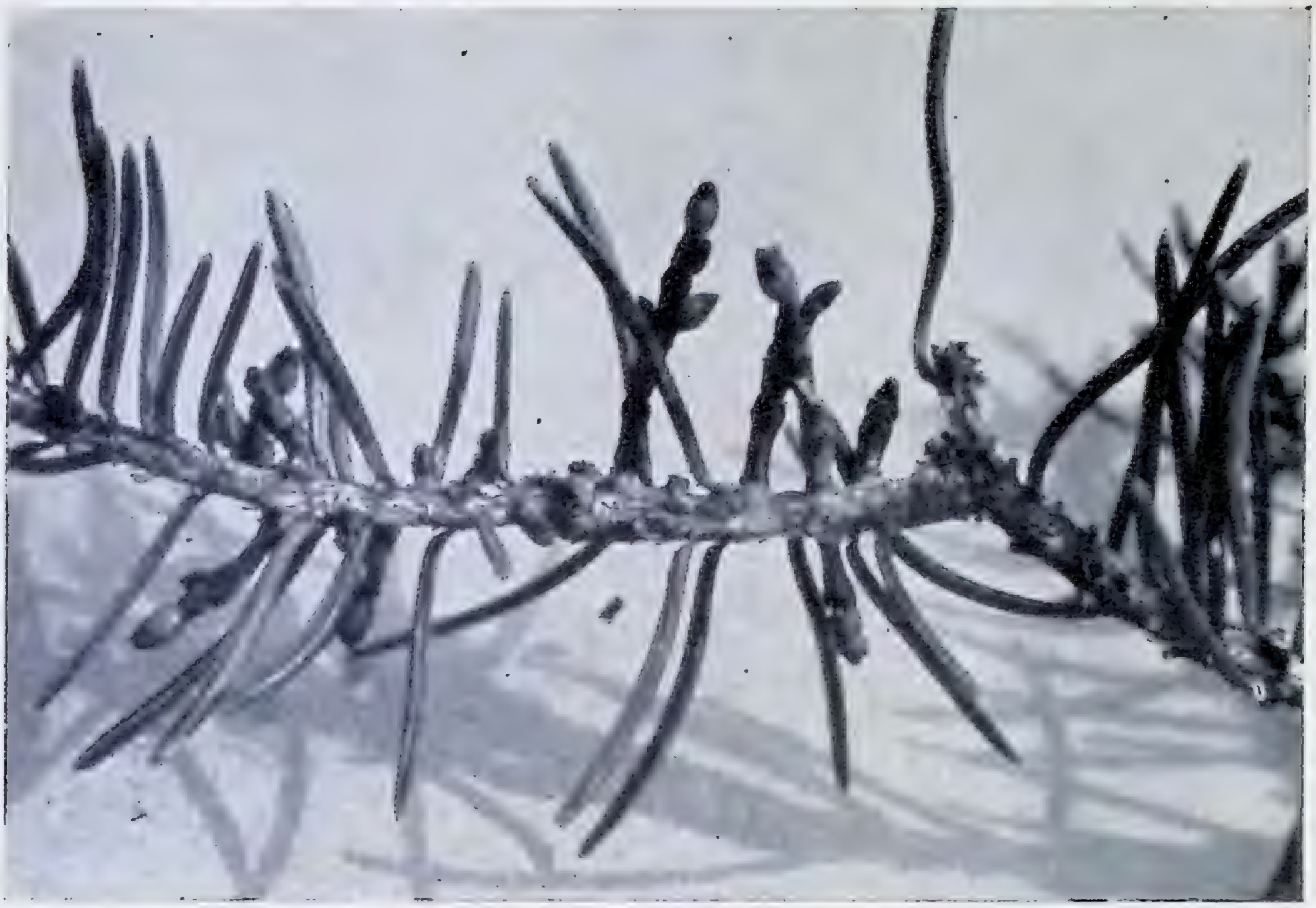

FIGURE 3. *A. pusillum*, pistillate, on *Picea glauca*

map is based are apparently no more extant, and the data can therefore be incorporated only tentatively in the present map. The collection and proper preservation of specimens from these localities is of considerable importance. A later report by Zalasky (1956) extends the known northern limits of *A. americanum* to Black Birch and Careen lakes in Saskatchewan.

Western limits seem to coincide approximately with the summit of the Coast Range (Kuijt, 1956) which, in turn, corresponds to the line separating *Pinus contorta* subsp. *contorta* from subsp. *latifolia* (Critchfield, 1957). Here, as in California, the western limit of *A. americanum* is probably determined by factors relating to forest history and ecology, and not by an inherent difference in susceptibility between the two subspecies of lodgepole pine.

Pinus banksiana and *P. contorta* are the most common hosts. A few scattered infections on *P. ponderosa* have been noted (Kuijt, 1953). The rather unexpected transfers to *Picea glauca* first described by Bourchier (1953) are now known from several localities, all within the Albertan Rocky Mountains. The fact that the latter two hosts, when infected, are always in the vicinity of infected *P. contorta* indicates the inability of *A. americanum* to perpetuate itself within a pure spruce stand. This inference agrees with the scarcity of mistletoe shoots at least on the brooms of *Picea glauca* (Kuijt, 1960*b*). It is apparently only in its parasitism on *Pinus banksiana* and *P. contorta* that the mistletoe can be sufficiently prolific to allow it to maintain itself as a population.

The proposition that *A. americanum* does not occur west of the Coast Range needs to be defended against two literature references to the contrary. Macoun (1886), first of all, reports the species "On *Pinus contorta* at Victoria, Vancouver Island." The Dawson specimen, upon which this citation rests, is, in all probability, Dawson 23783 (CAN), "Vancouver Island," collected on Aug. 20, 1876. This specimen is unquestionably *A. campylopodum*. The latter species has since been collected on lodgepole pine in several localities near Victoria. Elsewhere (Foster and Ziller, 1952) a map has been printed showing some stations for *A. americanum* on Vancouver Island. The specimens concerned have since been checked and were found to be *A. campylopodum*.

A. campylopodum Engelmann

Hemlock mistletoe, larch mistletoe Figure 2b

Specimens Seen: (host abbreviations as follows: Aa—*Abies amabilis;* Al—*Abies lasiocarpa;* Lo—*Larix occidentalis;* Pc—*Pinus contorta;* Pe—*Picea engelmannii;* Pm—*Pinus monticola;* Th—*Tsuga heterophylla*)

British Columbia: Anon., Arrow Lakes: Burton (DAO), Pc; Anon., Cortes Island (DAVFP), Th; Anderson, hill near Saseenos, Sooke (V), Pc; *idem,* Sechelt (V), Th; Andrews & Grant, St. Marys River road near Cranbrook (DAVFP), Al; Bayliss, Crawford Bay (UBC), Lo; Bennett 25, Sooke, 200 ft. (K), Pc; Boys, northeast Texada Island (V), Th; Browne, Kitsum Kalum Lake, Terrace (DAVFP), Aa; Calder & Savile 11415, 3 mi. north of Moyie along highway (NY, V, WTU), Lo; *idem* 11465, 6 mi. along road to Cascade from junction just west of Rossland (UBC), Lo; Collis, Lund (DAVFP), Th; *idem,* south side of Khartoum Lake, 500 ft. (DAVFP), Th; *idem,* southwest end of Lois Lake, Lund (DAVFP), Th; Davidson 2091, Savary Island (UBC), Pc; Eastman, Moketas Island, Kyuquot Sound, sea level (UBC), Th; Foster, Nelson (DAVFP), Lo; *idem,* Cameron Lake, 600 ft. (DAVFP), Th; *idem,* Courtenay (DAVFP), Pc; Fraser, Ucluelet (CAN, UBC), "Douglas fir" (probably Th); Grant, 15.3 mi. north of Grand Forks (DAVFP), Pe; *idem,* Edgewood (DAVFP), Pc; *idem,* 5 mi. south of Fauquier (DAVFP), Pc; *idem,* 34 mi. north of Grand Forks (DAVFP), Al; Grant & Andrews, 16.4 mi. east of Christina Lake (DAVFP), Al; Grant & Wood, 2 mi. east of Christina Lake on new highway (DAVFP), Pc; Grismer, Mackinson Flats, near West Arrow Park (DAVFP), Lo; Henson, Capilano Valley, North Vancouver (DAO), Th; Jardine, Wilson Creek, Jackson logging road, 2.4 mi. from highway (DAVFP), Pc; Kuijt 543, north of Creston (CFB, UBC), Lo; *idem* 544, St. Marys Lake (CFB, UBC), Lo; *idem* 546, north of Castlegar (CFB, UBC), Lo; *idem* 547, Salmo (CFB, UBC), Lo; *idem* 548, 549, 552, Fruitvale (CFB, UBC), Lo; *idem* 550, south of Salmo (CFB, UBC), Lo; *idem* 551, north of Salmo (CFB, UBC), Lo; *idem* 553, Christina Lake (CFB, UBC), Lo; *idem* 554, Slocan Lake (CFB, UBC), Pm; *idem* 556, Grand Forks (CFB, UBC), Lo; *idem* 563, Balfour (CFB, UBC), Lo; *idem* 565, Needles (CFB, UBC), Pc; *idem* 566, Burton (CFB, UBC), Lo; *idem,* Happy Valley, near Victoria (CFB), Pc; *idem,* 2 mi. west of Parksville (DAVFP), Pc; *idem*, Horne Lake (CFB), Pm; *idem* 2387, 5 mi. east of Hope, along Hope-Princeton highway (UBC), Th; *idem* 2388, Zoo area, Stanley Park, Vancouver (UBC), Th; *idem* 2389, hedge, botanical gardens, UBC, Vancouver (UBC), Th; MacBean, Cowichan Lake, near Expt. Sta. (V), Th; Malkin, Bowen Island (UBC), Th; Monaghan, Sayward: Coulter Bay, 10 ft. (DAVFP), Th; Porter, Sayward (DAVFP), Th; Rawlins, Errington, near Parksville (V), Pc; Rosendahl 1958, Sproat Lake, Vancouver Island (GH, K, NY), Pc; *idem* 60280, Vancouver Island, District of Renfrew; possibly the type of *A. tsugensis* Rosendahl ? (CAN), Th; Ruppel, Nakusp (DAVFP), Lo; *idem*, Squamish: Stawamus Creek (DAVFP), Aa; Ruppel & Jardine, Cypress Creek, Port Moody (DAVFP), Aa; Taylor & Harvey, Dashwood, Vancouver Island (DAVFP), Pc; Toms, Shawnigan District (V), Pc; Ziller, near Summit, Mt. Finlayson (DAVFP), Pc.

WASHINGTON: The following collection is added for interest's sake: Zeller & Zeller 1194, Mt. Constitution, Orcas Island; cited as f. *campylopodum* in Gill's (1935) treatment (GH, K, NY), Pc.

DISCUSSION

The distribution of *A. campylopodum* in British Columbia falls neatly into two separate major areas. The restriction of larch mistletoe to the interior is not surprising as western larch does not occur west of the Okanagan Valley. More unexpected is the coastal distribution of the hemlock mistletoe, the interior hemlock zone being apparently free of the parasite. Whether these areas of *A. campylopodum* are actually disjunct can be ascertained only by study of material from south of the border. From Gill's treatment it can be seen that a scattering of localities of hemlock mistletoe is known from Idaho and interior Washington, but these collections are too widely spaced to form any obvious pattern.

It must be admitted that hemlock mistletoe has been reported from the Upper Columbia region of the province (Foster, *et al.*, 1954). No collection supporting this report, however, is present in any of the herbaria consulted in this study. In my own travels in the Big Bend region and other parts of the interior hemlock zone, I have been unable to find evidence of mistletoe infection on hemlock, even when growing directly below larch overstory heavily infected with *A. campylopodum*. In the absence of specimens, therefore, I assume the interior hemlock of the province to be free of mistletoe.

The coastal hemlock mistletoe has been very incompletely collected because of difficulties in terrain and climate. The scattering of collections, nevertheless, seems to indicate that no major interruptions exist in its coastal distribution from Washington (cf. Gill, 1935) to Alaska (cf. Anderson, 1946). Although no mistletoe collections from the Queen Charlotte Islands seem to be extant, the photographs in Foster and Foster (1951) leave little doubt as to its existence there. *A. campylopodum* also occurs in rather extensive populations on lodgepole pine, *Pinus contorta*, in dry sites where this tree predominates from Orcas Island (Washington) and Victoria north to Cortes Island. From the latter host, *A. campylopodum* is

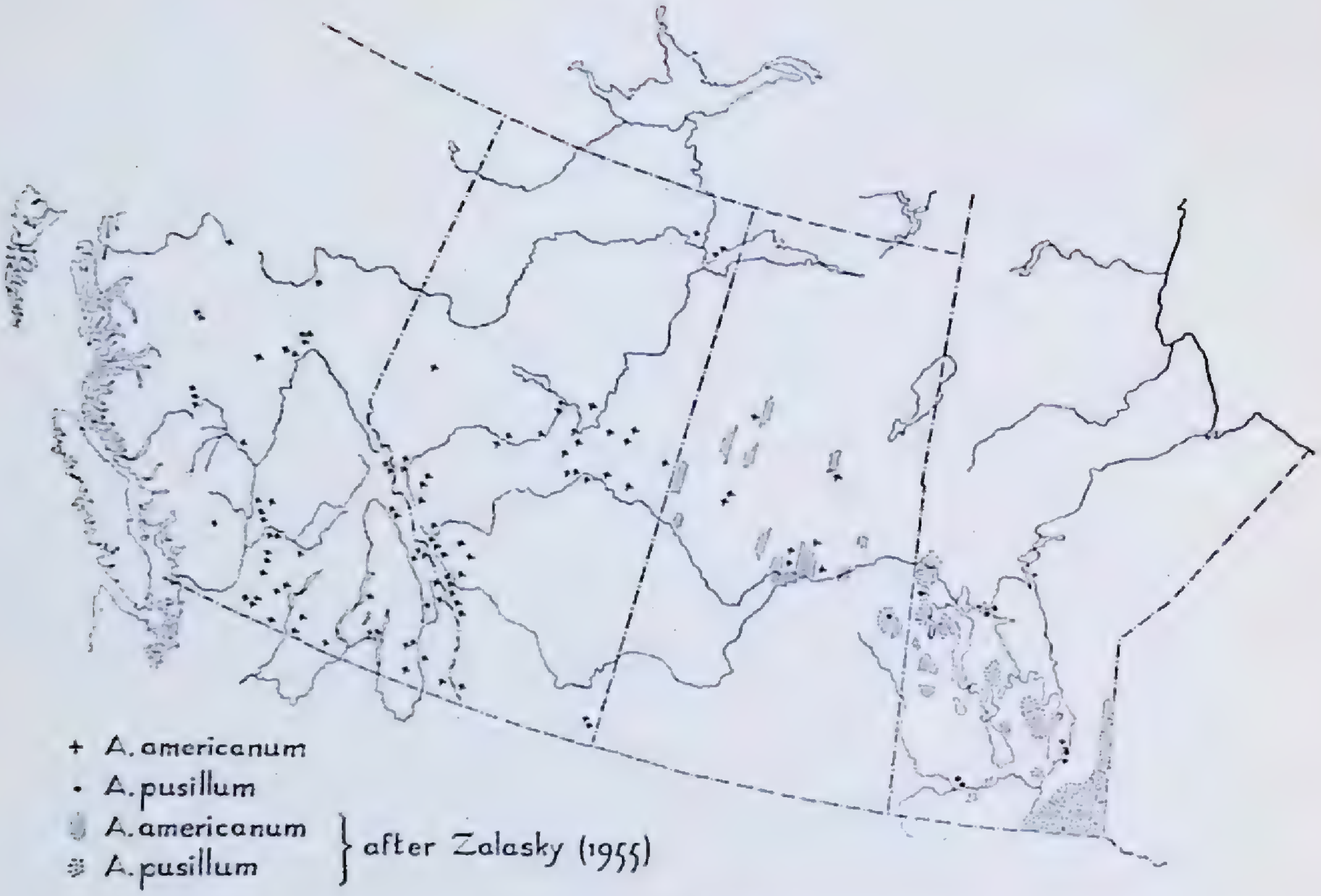

FIGURE 4. Geographic distribution of *A. americanum* and *A. pusillum*

known to be transferable to individuals of western white pine, *Pinus monticola* (Kuijt, 1961), but whether transfers can take place between these pines and hemlock has not yet been established.

The mistletoe on larch and its apparent transfers to *Abies, Picea,* and *Pinus* is thus restricted by the Rocky Mountain trench to the east and the Okanagan Valley to the west. Its northward limits are not firmly established at present but may not differ materially from the pattern evident from the map. The extensive stands of larch on the western slopes of the Rocky Mountains appear to be quite free of the parasite.

Gill (1935, p. 186) claims that his *A. campylopodum* f. *campylopodum,* presumably on Ponderosa pine (*P. ponderosa*), extends into Canada. This appears not to be correct. The nearest locations in the United States, judging from Gill's citations, are Kettle Falls and Omak, Washington. *A. campylopodum* on Ponderosa pine has not as yet been recorded from Canada. It is possible that Gill's statement rests on Macoun (1886), who erroneously writes of "*A. robustum*" (a synonym of *A. vaginatum* (Willd.) Presl from the Southwest) on Ponderosa pine from "Kootanie Valley, near Columbia Lakes, 1883." I have seen only Dawson 23785 (CAN) from Elk River, "Kootanie Valley," collected in 1883. The latter specimen is undoubtedly *A. americanum,* growing on lodgepole pine. I suspect that Macoun's reference is based on the same species of mistletoe that transfers sporadically to Ponderosa pine in this and other areas. At any rate there is no substantial evidence of *A. campylopodum* having been found on Ponderosa pine in the province.

A. douglasii Engelmann

Douglas fir mistletoe Figure 2c

Specimens Seen: (host abbreviations: Ag—*Abies grandis;* Pm—*Pseudotsuga menziesii*)

British Columbia: Calder & Savile 10184, 8 mi. northwest of McCulloch, southeast of Kelowna (DAO, UBC), Pm; *idem* 11413, 1 mi. south of Sirdar, north of Creston (DAO, UBC, WTU), Pm; *idem* 11536, bluffs west of Summerland Expt. Sta. (DAO, UBC), Pm; Eddie, Wood Lake, 20 mi. north of Kelowna (UBC), Pm; Kuijt 650, 10 mi. north of Sirdar (CFB, UBC), Pm; *idem* 580, Beaver Lake road, near Wood Lake (CFB, UBC), Pm; *idem* 581, Destiny Bay, Kootenay Lake (CFB, UBC), Ag; *idem* 601, Big Sheep Creek (CFB, UBC), Pm; *idem* 2381, Sirdar, near Creston (DAVFP, UBC), Pm; *idem* 2382, Yellow Lake (UBC), Pm; *idem* 2383, Okanagan Campsite, north of Penticton (UBC), Pm; Taylor 1301, Cathedral Lakes, Ashnola District (UBC), Pm; Thomas and Foster, Keremeos, 2,000 ft. (DAVFP), Pm.

Discussion

The Douglas fir mistletoe in British Columbia occupies only a fraction of the range of its major host, Douglas fir (*Pseudotsuga menziesii*). It follows, first of all, Kootenay Lake from near Creston to Destiny Bay. The Okanagan population reaches from Anarchist Mountain north to Wood Lake, with an extension westward past Keremeos and even into the Ashnola Valley. I am not sufficiently acquainted with the situation in the adjacent parts of the United States to say whether these two Canadian populations represent two disjunct areas separated by a hundred miles of mountainous territory. It is certain that Douglas fir mistletoe is common in areas south of the International Boundary near Creston (Graham, 1960). The collection at Big Sheep Creek was obtained from one of two infected trees in an otherwise apparently healthy area. In this case, continuity across the border seems to be out of the question. This pair of infected trees, one old and heavily broomed, the other belonging to the understory, almost fifty miles from the nearest Douglas fir mistletoe, may well be a result of long-distance spread by birds.

A. douglasii is, therefore, a species which does not inhabit coastal areas, not only in its northern range, but also in its southern distribution pattern (Kuijt, 1960*a*). This absence from coastal areas, interestingly enough, is echoed in the distribution of *A. americanum* (*see* above). Ecological and historical factors, rather than differences in susceptibility on the part of the hosts, are perhaps responsible for both patterns.

A. pusillum Peck

Spruce mistletoe Figure 3

Specimens Seen: (all on *Picea glauca*)

Manitoba: Anon., Spruce Woods Reserve east of Brandon (WIN); Bisby, Victoria Beach (WIN); Jackson, Grand Rapids (WIN); Löve &

Löve 6262, sand dunes 15 mi. south-southeast of Carberry (CAN, SASK, UBC, WIN);

SASKATCHEWAN: Kuijt 2378, 24 mi. east of first junction south of Hudson Bay (UBC).

DISCUSSION

The spruce mistletoe is a predominantly eastern species (cf. Gill, 1935). Since most of its natural range, therefore, falls outside the area here considered, little can be said about the distribution pattern in its western extremity. The vegetational continuity of the coniferous belt reaching across the Prairie Provinces leads one to wonder why *A. pusillum* is not found west of Hudson Bay, Saskatchewan, where many hundreds of miles of spruce territory remain free of this parasite. The possibility of an imperceptibly slow migration being in progress can, of course, not be excluded.

Zalasky's (1955) data have been added to the map in a complementary fashion; again, specimens for these stations are no longer available.

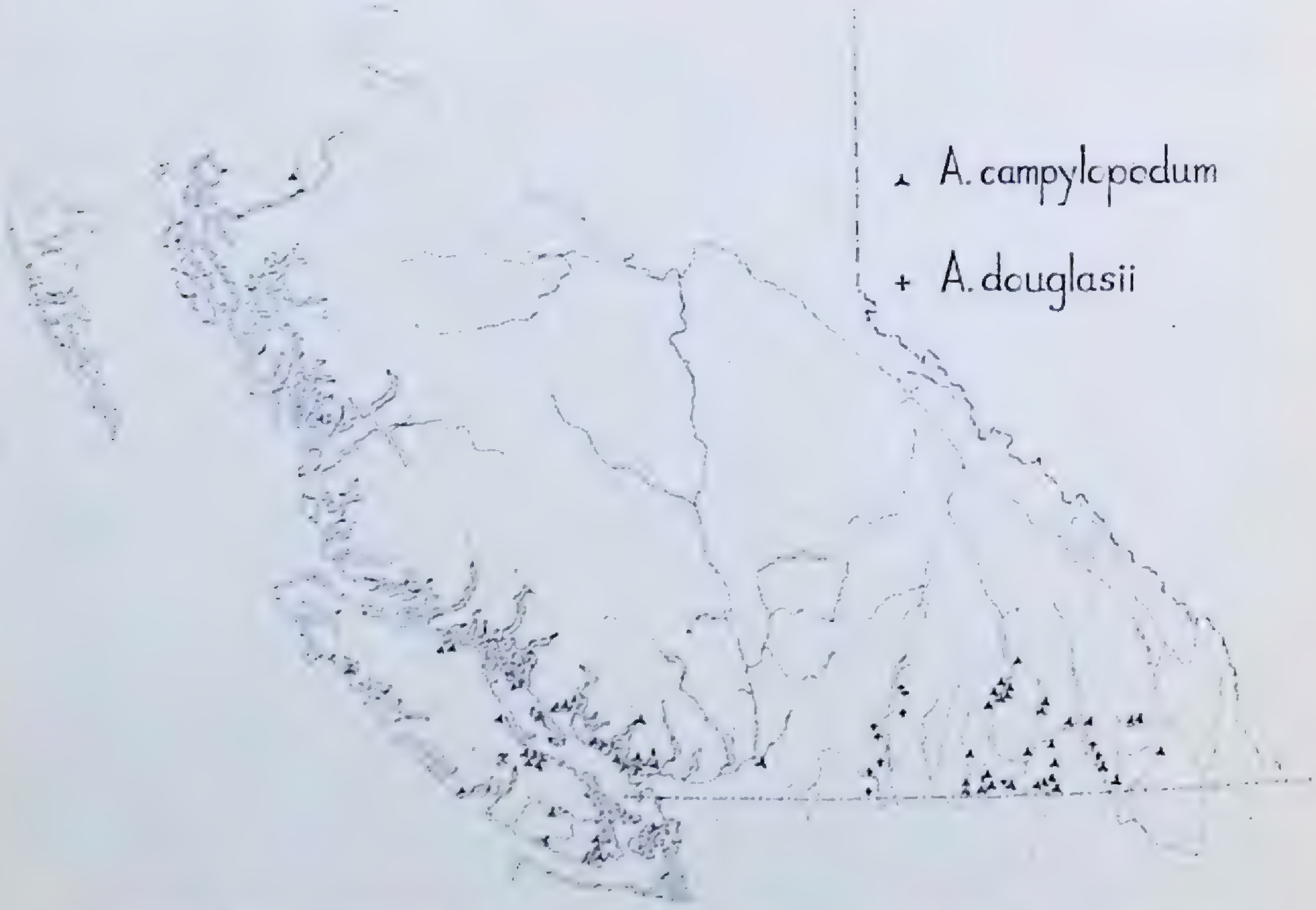

FIGURE 5. Geographic distribution of *A. campylopodum* and *A. douglasii*

DISTRIBUTION OF HYPERPARASITIC FUNGI ON DWARF MISTLETOES

Wallrothiella arceuthobi (Peck) Saccardo

Wallrothiella arceuthobii, a most curiously specialized parasitic fungus on dwarf mistletoes, has been reported from a number of localities within our range (Dowding, 1931; Kuijt, 1955; *see* especially Thomas, 1953). The fungus, a member of the *Spaeriales,* attacks the pistillate flowers only, destroying all internal tissues and preventing the normal development of the fruit. A black stroma is formed in the stigmatic region, bearing a number of perithecia. Neither the remainder of the pistillate plant nor any part of the staminate plant are attacked. Illustrations may be seen in the first two of the above-mentioned papers. Material from the following localities has been seen:

On *Arceuthobium americanum*: (Pb—*Pinus banksiana;* Pc—*Pinus contorta;* Pg—*Picea glauca*):

Bourchier, Jasper, Alta. (CFB), Pc; *idem,* Vermilion Crossing, Kootenay National Park, B.C. (CFB), Pc; *idem,* Kootenay Crossing, Kootenay National Park, B.C. (CFB), Pc; *idem,* Snaring River, Jasper National Park, Alta. (CFB), Pg; *idem* & Kuijt, Mi. 9 Settler's Road, Kootenay National Park, B.C. (CFB), Pc; Breitung 8430, Waterhen Forest Reserve, 50 mi. north of Meadow Lake, Sask. (DAO), Pb; Glen, Emma Lake, Sask. (UBC), Pb; Jackson, Mile 62, Grand Beach, Man. (WIN), Pb; Kuijt 508, Kananaskis, Alta. (CFB), Pc; *idem* 512, Whitecourt, Alta. (CFB), Pb; *idem* 527a, Kimberley, B.C. (CFB, UBC), Pc; *idem* 533, Mi. 7 Medicine Lake road, Jasper National Park, Alta. (CFB, UBC), Pc; *idem* 535, Yellowhead, B.C. (CFB), Pc; *idem* 537, Mi. 10.3 Edith Cavell road, Jasper National Park, Alta. (CFB, UBC), Pc; *idem* 568, Bull River, B.C. (CFB, UBC), Pc; *idem* 2385a, banks of Thompson River 5 mi. west of Chase, B.C. (UBC), Pc; *idem,* at Radium Hot Springs, B.C. (DAVFP), Pc; Loman & Wilkinson, Owl River, 23 mi. north of Lac La Biche, Alta. (CFB), Pb; Patterson, 17 mi. northeast of Ft. Assiniboine, Alta. (CFB), Pb; Taylor, Vanderhoof, B.C. (DAVFP), Pc; Thomas, Prince Albert, Sask. (CFB), Pb; Ziller, Merritt, B.C. (DAVFP), Pc.

On *Arceuthobium douglasii:* (both on *Pseudotsuga menziesii*):

Kuijt 588, 10 mi. southeast of Kelowna, B.C. (CFB, UBC); *idem* 2381, Sirdar, near Creston, B.C. (DAVFP, UBC).

Wallrothiella has been reported from the western United States on *Arceuthobium americanum, A. douglasii, A. campylopodum* f. *abietinum* and f. *microcarpum* (Weir, 1915; Gill, 1935). Infection of the pistillate flower probably occurs during the receptive stage (Dowding, 1931) immediately after fertilization of the egg cell.

It would be remarkable if this exceedingly specialized fungus were to parasitize both spring- and fall-flowering dwarf mistletoes. It is improbable, though not impossible, that two overlapping life cycles exist within *Wallrothiella* to make this possible. Scrutiny of literature reports of infected *A. campylopodum* raises doubts as to the proper identification of the mistletoe specimens concerned. Weir (1915) speaks not of *A. campylopodum* but of *A. douglasii* var. *abietina* and var. *microcarpa*. Both his remarks and photographs make it clear that the mistletoes, in fact, are *A. douglasii* in their infrequent occurrence on species of *Abies* and *Picea*. This leaves only Gill's (1935, p. 220) reference to parasitism on *A. campylopodum* f. *abietinum* to be accounted for. Here, also, an apparent association with *A. douglasii* makes the identification suspect. We can conclude, therefore, that in all probability *Wallrothiella arceuthobii* is restricted to the spring-flowering species *A. pusillum*, *A. americanum*, and *A. douglasii*. Such a conclusion receives further support from the geographical distribution of the hyperparasite.

Septogloeum gillii Ellis

Although *Septogloeum gillii* (Fungi Imperfecti) periodically devastates dwarf mistletoe in some Canadian localities, the fungus was not reported from Canada until recently (Bourchier, 1954). The collections cited below demonstrate the fact that this fungus has a wide distribution in the western part of Canada; it has not as yet been reported from *A. pusillum* in any of its eastern or midwestern stations.

A word of warning is necessary here. The identification of *S. gillii* in the specimens below may not always be reliable. In some cases the characteristics of the fungus do not seem to agree with Ellis's (1946) original description. The more conspicuous yellowish-white lesions with masses of hyaline spores often seem to originate as small blackish warts on the host. Variation of spore characteristics throughout this cycle is insufficiently known and is probably responsible for some difficulties in identification. The citations below, therefore, should be taken only as tentative identifications.

Specimens Seen: (host abbreviations as follows: Lo—*Larix occidentalis;* Pb—*Pinus banksiana*; Pc—*Pinus contorta*; Pme—*Pseudotsuga menziesii*; Pmo—*Pinus monticola*; Th—*Tsuga heterophylla*)

On *Arceuthobium americanum:*

Bourchier, Seebe, Alta. (CFB), Pc; *idem*, Jasper, Alta. (CFB), Pc; *idem*, Jasper airfield (CFB), Pc; *idem*, Hawk Creek, Kootenay Nat. Pk., B.C. (CFB), Pc; *idem*, Smoky Lake, Alta. (CFB), Pb; Calder, Parmelee & Taylor 18770, 5 mi. south of Jesmond along road to Kelly Lake, B.C. (DAO), Pc; Glen, Emma Lake, Sask. (UBC), Pb; Kuijt 501, Old Golf Course, Banff, Alta. (CFB), Pc; *idem* 508. Kananaskis, Alta. (CFB), Pc; *idem* 528, Windermere, B.C. (CFB, UBC), Pc; *idem* 533, Mi. 7, Medicine Lake road, Jasper National Park, Alta. (CFB, UBC), Pc.

On *Arceuthobium campylopodum*:

Kuijt 554, Slocan Lake, B.C. (CFB, UBC), Pmo; *idem* 562, Slocan Lake, B.C. (CFB, UBC), Lo; *idem* 602, Metchosin, B.C. (CFB, UBC), Pc; *idem* 605, 12 mi. north of Qualicum Beach, B.C. (CFB, UBC), Th; *idem*, 2 mi. west of Parksville, B.C. (DAVFP), Pc.

On *Arceuthobium douglasii:*

Kuijt 580, Beaver Lake road near Wood Lake, B.C. (CFB, UBC), Pme; *idem* 588, 10 mi. south of Kelowna, B.C. (CFB, UBC), Pme.

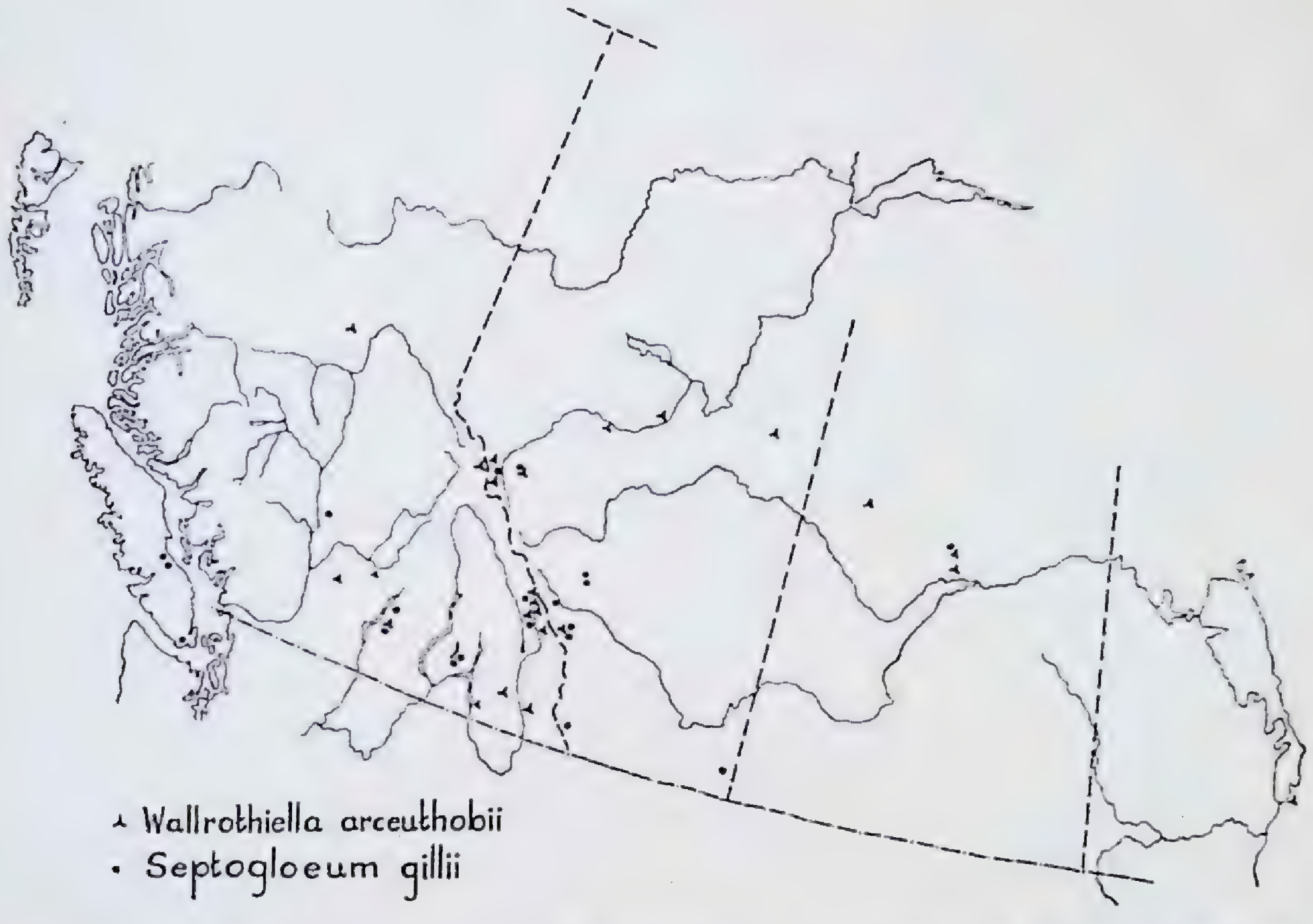

FIGURE 6. Geographic distribution of *Wallrothiella arceuthobii* and *Septogloeum gillii*

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